Phenotypic differentiation in the Azorean woodpigeon (*Columba palumbus azorica*)

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Mestrado em Ecologia e Ambiente

Departamento de Biologia

2017

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Todas as correções determinadas
pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, _____/_____/_____

Acknowledgements

I would like to express my gratitude to all that helped me during this thesis especially Prof. David Gonçalves and Pedro Andrade for the amazing support, for all the things they taught me and for the personal and professional development for which they contributed enormously both now and when I did the bachelor internship with them two years ago. I would also like to thank Prof. David Gonçalves for the opportunity to work in this interesting project opening me the doors to the research in evolution, ecology and how morphology can tell us so much about the history and ecology of a species, areas of interest which together with wildlife management and conservation led me to biology five years ago. I would also like to thank him for constantly offering his support and supervision, for the patience and for trusting me. I would like to thank Pedro Andrade for the overwhelming support and knowledge transmission, having been an incredible pillar in the execution of this work and for giving me access to his database on woodpigeon external biometrics. I would also like to thank Tiago M. Rodrigues for the advices regarding some laboratorial parts of this work.

I would like to thank to the following persons and institutions for their involvement in the process of collection of specimens: *Direção Regional dos Recursos Florestais* (Azores), in particular to Manuel Leitão; *Direção Regional do Ambiente* (Azores), in particular to Emanuel Veríssimo; João Queirós, Tiago M. Rodrigues and Rémi Fontaine (CIBIO-InBIO); Thomas Kjær Christensen (Aarhus University; Denmark); Yves Ferrand, Hervé Lormée, Jean-Michel Vasseur, Hervé Bidault, Luc Tison, Benjamin Calmon (Office national de la chasse et de la faune sauvage, France); Miguel Minondo Verdú, Raúl Costillas (Spain).

I also would like to thank to *Direção Regional da Ciência e Tecnologia* (Azores), for the financial support of the project "Ecology and evolution of the Azores woodpigeon: support tools for a management and conservation strategy" (AZORPI) (M2.1.2/I/025/2011) that was at the origin of the present study. Also I must thank Maria Amélia Fonseca and Verónica Neves, researchers from the University of Azores, respectively principal investigator and team member of the AZORPI project. I would like to thank Francisco Moreira for the help in the preparation of some specimens and Professor Nuno Formigo for the availability to clarify doubts and for the important advices given during the last two years.

I would also like to thank all my friends and family for the company and support.

Abstract

Across the geographical range of a species, different morphological answers rise in response to changing adaptive needs. The adaptation to the insular environment is well known as a driver of phenotypic change in birds, and several well-known patterns have been described in several phenotypic traits such as colour (decreased ornamentation and sexual dimorphism) and morphology (changes in size, adaptation to sedentary life style, shape changes along with niche expansion). To gain more insight into these processes in birds, we studied patterns of colour and morphology change in the woodpigeon *Columba palumbus*, which has a sedentary insular subspecies (*C. p. azorica*), while the continental populations (*C. p. palumbus*) can either be sedentary or migratory. In this study, external and skeletal morphology, as well as colour patterns were compared between Azorean and continental birds, as well as between males and females.

Analysis of colour showed clear differences between the two subspecies, indicating that Azorean birds are darker than the continental subspecies, which could be due to the even more prominent decrease in ornamentation in islands or environmental conditions such as habitat luminosity. We also recovered a pattern of sexual dichromatism in the woodpigeon with male birds displaying higher UV chroma values than females. These differences are more pronounced in the continent which may show that there is a tendency for monomorphism in the insular environment.

No differences in overall body size was found between the two subspecies, but several morphological differences consistent with the adaptation to the insular environment were observed, particularly in bill size (longer bills), development of the flight apparatus (smaller pectoral girdle and shorter wings) and leg size (larger legs). These patterns underlie a tendency towards sedentarisation in the Azorean subspecies. Our results give preliminary support to the endemic subspecies taxonomic status of the Azorean woodpigeon.

Keywords: *Columba palumbus*, morphology, Azores, Continent, island rule, sexual dimorphism.

Resumo

Ao longo da distribuição geográfica de uma espécie, diferentes respostas morfológicas surgem em resposta a mudanças de necessidades adaptativas. A adaptação ao ambiente insular é conhecida como sendo um motor de mudanças fenotípicas em aves e vários padrões conhecidos foram já descritos em vários traços fenotípicos como a cor (ornamentação e dimorfismo sexual diminuídos) e a morfologia (mudanças de tamanho, adaptação a estilo de vida sedentário, mudanças de forma, juntamente com expansão do nicho). Para obter mais infirmações acerca desses processos em aves, estudámos padrões de cor e morfologia no pombo-torcaz *Columba palumbus,* que tem uma subespécie insular sedentária (*C. p. azorica*), enquanto as populações continentais (*C. p. palumbus*) podem ser sedentárias ou migratórias. Neste estudo, a morfologia externa e do esqueleto, assim como os padrões de cor foram comparados entre aves açorianas e continentais, bem como entre machos e fêmeas.

A análise de cor mostrou diferenças claras entre as duas subespécies, indicando que as aves açorianas são mais escuras do que a subespécie continental, o que pode ser devido à diminuição da ornamentação nas ilhas ou a condições ambientais como a luminosidade do habitat. Também foi percetível um padrão de dicromatismo sexual no pombo-torcaz, com machos a apresentar valores mais elevados de croma UV. Estas diferenças são maiores no continente, o que parece mostrar que existe uma tendência para o monomorfismo no ambiente insular.

Não foram encontradas diferenças no tamanho geral do corpo entre as duas subespécies, mas foram observadas várias diferenças morfológicas consistentes com a adaptação ao ambiente insular, particularmente no tamanho do bico (bicos mais longos), desenvolvimento do aparelho de voo (ossos da zona peitoral menores e asas mais curtas) e tamanho das patas (patas maiores). Estes padrões indicam uma tendência para a sedentarização na subespécie açoriana. Estes resultados dão suporte preliminar ao estatuto taxonómico de subespécie endémica do pombo-torcaz-dos-Açores.

Palavras-chave: *Columba palumbus*, morfologia, Açores, Continente, regra insular, dimorfismo sexual.

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Abbreviations

Bb – Basal breadth

Bd – Breadth of the distal epiphysis

Bp – Breadth of the proximal epiphysis

Db – Distal breadth

Did – Diagonal of the distal epiphysis

Dip – Diagonal of the proximal epiphysis

GL – Greatest length

SC – Smallest breadth of the corpus

1– Introduction

1.1 – Insularity and evolution of island birds morphology

Local environmental conditions are one of the key factors that influence the evolutionary trajectory of species. Consequently, populations from widely-distributed species usually display gradual changes in morphology and other traits along geographical gradients. This can be exemplified by Bergmann's rule, which states that in wide-ranging warm-blooded animal species, individuals living in a cold climate tend to be larger than individuals of the same species living in a warm climate, which usually means that body size increases with latitude (Mayr, 1956; Proctor and Lynch, 1993; Esteban and Ariño, 2000; Ashton, 2002; Yom-Tov, 2003; Rodríguez *et al.*, 2008; Freeman, 2017). Another example is Allen's rule, which postulates that in warm-blooded animals with a wide distribution, the limbs, ears, and other appendages of individuals of populations living in warmer climates tend to be larger than in animals of the same species living in cold climates. Longer and less compact body parts have more surface area than shortened ones and therefore lose more body heat (Ray, 1960; James, 1983; Nudds and Oswald, 2007).

Since the development of evolutionary theories, islands have been used as models to understand evolutionary processes due to their unique characteristics, as different selective forces from the ones that act on continental populations make the populations that inhabit them adapt in different directions from those in the mainland (Darwin, 1859). Islands have unique characteristics, not only in comparison to mainland but also between different islands, depending on their area and distance to the continent (Kadmon and Pulliam, 1993; Denslow, 2001; McNab, 2002; Lomolino, 2005; Losos and Ricklefs, 2009). As a result of the geographic isolation and small size of many islands, species diversity tends to decline in smaller and more isolated islands while population densities increase (Lomolino, 2005). These specific ecological characteristics of islands have been shown to have a strong effect on the morphological evolution of populations in this sort of geographical setting (Juan *et al.*, 2000), as they alter ecological factors and dynamics such as vegetation structure, food resources, predation, parasitism and species' life histories. One such life history trait that changes in insular populations, specifically of birds, is migration. Numerous populations that reside the mainland migrate for long distances while insular populations of the same species tend to be sedentary, reducing dispersal ability over time or even leading to flightlessness (McNab, 2002, Wright *et al.*, 2016).

Islands are regularly inhabited by populations of species closely associated to nearby continental groups but frequently there are differences in body size between insular and continental populations, as small bodied species (such as rodents or small birds) typically evolve to larger sizes in islands (island gigantism), whilst larger bodied species (like some carnivores, primates, lagomorphs and artiodactyls) are normally smaller in islands (island dwarfism) (Foster, 1964; Grant, 1965; Van Valen, 1973; Damuth, 1993; Adler, 1994; Clegg and Owens, 2002; Millien and Damuth, 2004; Lomolino, 2005; Boback, 2006; McClain *et al.*, 2006; Raia and Meiri, 2006; Bromham and Cardillo, 2007; Clegg *et al.*, 2008; Meiri *et al.*, 2008; Weston and Lister, 2009; Benton *et al.*, 2010; Boyer and Jetz, 2010; Roulin and Salamin, 2010; Wright and Steadman, 2012; McClain *et al.*, 2013; Melo *et al.*, 2017). This tendency is known as "island rule" (Van Valen, 1973). There are also evidences from insular animals, such as birds, that body size tends to increase with the area of the island and to decrease with the distance to the continent (Carrascal *et al.*, 1994; Rising, 2001; Clegg and Owen, 2002; Förschler *et al.*, 2008; Mathys and Lockwood, 2009; Boyer and Jetz, 2010; Roulin and Salamin, 2010; Wright and Steadman, 2012).

Some set of factors thought to be responsible for the island rule have been theorized, namely resource limitation, intensified intraspecific competition, ecological release and immigrant selection (Lomolino, 2005). On islands, the space that populations of a species can occupy is smaller, leading to an augmented population density. Therefore, there is an increased intraspecific competition for restricted resources, so larger animals tend to become smaller for better resource management, reducing energy expenses and decreasing their metabolism to do so (McNab, 2002; Lomolino, 2005), while smaller animals tend to evolve larger sizes for a possible benefit in intraspecific dispute and the possibility to spend longer times without resource consumption (Reyment, 1983; Lomolino, 1984; Clegg and Owens, 2002; Scott *et al.*, 2003; Lomolino, 2005). Besides resource limitation and intraspecific disputes, ecological release from interspecific forces may also be a potential selective pressure towards size or shape changes. In habitats with poorer communities like the ones on islands, the lack of predators and overall low rate of interspecific competition allow large vertebrates to adapt to the ecological simple communities present on islands reducing their metabolic rates by reducing the body size, while small animals can develop larger sizes due to the lack of necessity to avoid predators (Damuth, 1993; McNab, 1994; Rising, 2001; Lomolino, 2005; Noakes *et al.*, 2013). The absence of competitors and predators gives the colonizers the chance to better exploit the available resources (Brown *et al.*, 1993; Damuth, 1993). Island gigantism can also be

explained by immigrant selection, that is selection for the more vagile individuals since larger individuals tend to disperse more easily and to further away and to spend more time without food, acting mostly in the early stages of colonization of islands (Lomolino, 1984; Lomolino, 2005). Despite the evidence supporting the island rule, there are authors that suggest that it is not a pattern for all vertebrates and that there is no evolutionary driver towards a specific ideal size on islands (Meiri *et al.*, 2004; Meiri *et al.*, 2006; Meiri *et al.*, 2008; Raia *et al.*, 2010; Wright and Steadman, 2012; McClain, 2013; Itescu *et al.*, 2014; Karagkouni, *et al.*, 2017).

Numerous studies have focused on understanding what morphological changes are observed in insular versus continental bird species (Carrascal *et al.*, 1994; Fitzpatrick, 1998; Lomolino, 2005; Dietz *et al.*, 2007; Clegg *et al.*, 2008; Förschler *et al.*, 2008; Wright and Steadman, 2012). The foremost examples of morphological change in insular birds are related to one of their most characteristic traits, the ability to fly. The flight of birds has several implications on their fitness, due to its high energetic demands in order to counter gravity and drag, especially in migratory individuals (Hedenström, 1993; Hedenström, 2010). These demands are usually counterbalanced by behavioral, physiological and morphological adaptations (Viscor *et al.*, 1985; Piersma *et al.*, 2005; Butler, 2016; Vágási *et al.*, 2016). Among them, short hindlimbs (Winkler and Leisler, 1992; Tellería and Carbonell, 1999; Milá *et al.*, 2008), big pectoral girdle (Proctor and Lynch, 1993; Calmaestra and Moreno, 2000; Tobalske and Biewener, 2008; Kaiser, 2010) and hollow and pneumatic bones (Hogg, 1984; Casinos and Cubo, 2001; Wedel, 2005), increase aerodynamic performances, and reduce the weight of the skeleton (Proctor and Lynch, 1993; Hedenström, 2002; Tobalske and Biewener, 2008). According to some studies (Lomolino, 2005; Wright and Steadman, 2012), the lack of resources in islands in comparison to continental habitats induces vertebrates to preserve energy by reducing the metabolic rate. This possibility, allied to the knowledge that larger pectoral muscles are related to flight power, and that insular populations are usually sedentary, may explain small pectoral muscles and thus smaller sternum in insular populations (Proctor and Lynch, 1993; McNab, 2002; Lomolino, 2005; Dietz *et al.*, 2007; Wright and Steadman, 2012), as well as smaller flight apparatuses and shorter wings in islands birds, which could also be related to less interspecific competition and predation (Grant, 1965; Winkler and Leisler, 1992; Senar *et al.*, 1994; Lockwood *et al.*, 1998; Berthold, 1999; Copete *et al.*, 1999; Roulin and Salamin, 2010). A shorter flight apparatus can also allow insular birds to have more manoeuvrability, which is important in low-speed flight and in dense habitats, in opposition to mainland birds, especially migratory ones, which tend to have high aspect ratios (Winkler and Leisler, 1992; Lockwood *et al.*, 1998; Voelker, 2001; Fiedler, 2005)

and develop longer and more pointed convex wings, which increase flight efficiency (Lo Valvo *et al.*, 1988; Winkler and Leisler, 1992; Senar *et al.*, 1994; Mönkkönen, 1995; Fitzpatrick, 1998; Lockwood *et al.*, 1998; Berthold, 1999; Copete *et al.*, 1999; Tellería and Carbonell, 1999; Pérez-Tris and Telleria, 2001; Rising, 2001; Voelker, 2001; Egbert and Belthoff, 2003; Fiedler, 2005; Piersma *et al.*, 2005; Bowlin and Wikelski, 2008; Förschler *et al.*, 2008; Hedenström, 2008; Milá *et al.*, 2008; Förschler and Bairlein, 2011; Outlaw, 2011; Andrade *et al.*, 2015). It has also been shown that the wings from continental migrants tend to be bigger than those from continental residents, which in turn tend to be bigger than those from insular populations (Fitzpatrick, 1998; Förschler *et al.*, 2008). However, some studies show that insular birds may evolve longer wings in order to offset the reduced pectoral assemblage (Clegg *et al.*, 2008; Wright and Steadman, 2012).

Longer legs and foot span than in continental individuals are expected in island birds, linked to a more cursorial behaviour in insular individuals (Millener and Powlesland, 2001), while short hindlimbs are associated with reduced drag in continental ones, especially if migratory (Pennycuick *et al.,* 1996). The same for bigger and/or longer bills due to increase in niche breadth as a consequence of reduced interspecific competition for food and thus improving foraging diversity (Carrascal *et al.*, 1990; Carrascal *et al.*, 1994; Millener and Powlesland, 2001; Wright and Steadman, 2012; Leisler and Winkler, 2015). Other possible explanations may be related with intraspecific aggression and sexual selection (Luther and Greenberg, 2011).

According to some authors, mainland populations of birds, especially if migratory, have shorter and squarer tails than insular populations since they are more appropriate to reduce drag and increase the efficiency of forward flight; longer tails seem to be more beneficial to sedentary birds, which live in dense places, providing more manoeuvrability and compensating for smaller pectoral assemblage (Norberg, 1995; Thomas and Balmford, 1995; Pérez-Tris *et al.*, 1999; Voelker, 2001; Fiedler, 2005; Hedenström, 2008; Wright and Steadman, 2012). However, tail size may be under the influence of several selective pressures, including sexual selection, whereby the size of this structure must be analysed beyond its aerodynamic function (Fitzpatrick, 1999).

1.2 – Insularity and evolution of island birds colour

The colours of bird plumages are produced by a variety of pigments (melanins, carotenoids and porphyrins) and structural adaptations. These colours and patterns help birds in many ways, including as signals in mating rituals, UV radiation protection

and camouflage, are associated with the condition and/or social status of the individual, and other inter and intraspecific communication, having genetic and environmental bases (Proctor and Lynch, 1993; Pryke *et al.*, 2002; Jawor and Breitwisch, 2003; Alonso-Alvarez *et al.*, 2004; Quesada and Senar, 2006).

Environmental conditions, social interactions during the moult as well as various other occurrences, like range expansions, can modify sexual signals in birds (Price, 2006; Bro-Jørgensen, 2010; Cardoso *et al.*, 2014), and colour evolution can be independent in males and females (Price and Eaton, 2014). It would be expected that male birds would gain superior fitness benefits than females through multiple mating and consequently sexual selection should lead to the evolution of male-biased secondary sexual characters. Nonetheless, females of many species are also greatly ornamented as an outcome of sexual and social selection and not only as a result of changes in males. However, it has been shown that strong selection on males causes an increase in male colouration but a substantial decrease in female ornamentation (West-Eberhard, 1983; Amundsen, 2000; Rubenstein and Lovette, 2009; Tobias *et al.*, 2012; Dale *et al.*, 2015). It has been shown that sexual dichromatism may vary according to differences in mass, latitude, clutch size, social polygyny, sexual size dimorphism, migratory behaviour and type of parental care with sexual dichromatism decreasing with cooperative breeding, in which females display increased ornamentation (Avery *et al.*, 2014; Dale *et al.*, 2015).

Islands and continental conditions are different, affecting the intensity not only of natural but also of sexual selection (Badyaev and Hill, 2003). However, little is known about the effect of insularity in some traits such as colouration and to what degree plumage colour is part of the insularity syndrome. According to Uy and Vargas-Castro (2015) there is an increased occurrence of melanism in islands, especially in smaller ones. A pattern of less brightness (darker coloration) was also found in insular populations when compared to the continental counterparts of the same species (or closest relative), for both sexes, as well as lower number of patches (Grant, 1965; Fitzpatrick, 1998; Figuerola and Green, 2000; Rising *et al.*, 2009; Roulin and Salamin, 2010; Fabre *et al.*, 2012; Doutrelant *et al.*, 2016), but more significantly in males (Fitzpatrick, 1998; Fabre *et al.*, 2012; Doutrelant *et al.*, 2016). It has been demonstrated that there is less sexual dimorphism on islands, with bird species tending to develop monomorphic plumage across the sexes due to monogamy, increased population densities and biparental care (Badyaev and Hill, 2003; Roulin and Salamin, 2010; Doutrelant *et al.*, 2016), usually through reduced male ornamentation (Badyaev and Hill, 2003). Signal complexity (number of patches) is expected to be lower on islands due to the limited number of closely related sympatric species (Grant, 1965;

Figuerola and Green, 2000; Doutrelant *et al.*,2016), since signal differences should be more important in sympatric pairs of narrowly related species than in allopatric ones (Seddon, 2005; Martin *et al.*, 2010). This is in accordance with other studies (Martin *et al.*, 2010; Martin *et al.*, 2015) that suggest a pivotal role of interspecific interactions on colour pattern evolution at a community level.

These results show that insularity affects colour traits and the evolution of sexual dichromatism. However there are different patterns observed whereby the existence of a general insularity syndrome for colouration may not be plausible. Studies show that the decrease in signal intensity on islands is expected due to a decrease in the intensity of sexual selection due to the poorer indirect fitness profits of mate choice (Petrie *et al.*, 1998) and related reduction in extra-pair paternity (Hamilton and Zuk, 1982; Griffith, 2000) which may be caused from lower parasite pressure (one of the postulated reasons for the evolution of elaborate secondary sexual characters is to signal parasite resistance) (Hamilton and Zuk, 1982; Ishtiaq *et al.*, 2012), long term pair bonds (Figuerola and Green, 2000; Botero and Rubenstein, 2012) and reduced genetic diversity (Frankham, 1997; Griffith, 2000; Badyaev and Hill, 2003). The decrease in signal intensity may be also due to an increased parental care and longevity leading to reduced investment in costly signals (Figuerola and Green, 2000; Botero and Rubenstein, 2012; Covas, 2012).

There is also the possibility of indirect selection (pleiotropy) with selection acting on traits that are genetically correlated to colouration. For example, the melanocortin system also regulates aggressiveness, exocrine gland activity and energy homeostasis among other (Ducrest e al., 2008). Insular conditions exert selection on these traits (Stamps and Buechner, 1985; McNab, 2002; Müller *et al.*, 2007), so colour may evolve even if selectively neutral (Raia *et al.*, 2010; Roulin and Salamin, 2010).

According to Gloger's rule, animals that inhabit humid climates tend to be darker than those from dry areas, perhaps as an adaptation to different vegetation structure and habitat luminosity (Zink and Remsen, 1986; Proctor and Lynch, 1993; Burtt and Ichida, 2004; Cuthill, 2015; Roulin and Randin, 2015; Friedman and Remeš, 2017). Another explanation of Gloger's rule, in the case of birds, appears to be the increased resistance of dark feathers to feather-degrading bacteria (Burtt and Ichida, 2004). Grant (1965) tried to link Gloger's rule to differences in brightness in bird plumage between insular and continental individuals, but results were not conclusive.

Notwithstanding, the opposite has also been documented, with male and female birds with increased and brighter plumage ornamentation on islands although it is not the most prevalent situation (Avery *et al.*, 2014). Increased intra-sexual competition

over mates or food resources amongst females in sedentary populations can lead to increased ornamentation so it is one possible cause (West-Eberhard, 1983; Amundsen, 2000). Pleiotropy may also be an explanation for this atypical increase of brightness and ornamentation in islands (Raia *et al.*, 2010). Also, as previously stated, predation is reduced on islands which could relax selection for camouflage and promote elaboration and diversification of signals (Nachman *et al.*, 2003; Roulin and Wink, 2004; Raia *et al*., 2010; Runemark *et al.*, 2014).

1.3 – Biology and ecology of the woodpigeon and ecomorphology in columbiforms

The woodpigeon (*Columba palumbus* Linnaeus, 1758) (Figure 1) is a columbid (Columbiformes, Columbidae) with an exclusively Palearctic distribution, having an extensive distribution in Europe (including the Azores archipelago), Northern Africa and Western Asia (Baptista *et al.*, 1997; Gibbs et al., 2001). It is the biggest pigeon of Europe, reaching 45 cm in length and more than 600 g of weight, having a greyish plumage, duller on wings, mauve-pink breast merging to creamy on belly with iridescent purple-pink and green feathers beside a white patch on each side of the neck and a white patch on each wing. The plumage of juveniles is duller and without the white patch on the neck (Gibbs *et al.*, 2001). The woodpigeon displays very slight sexual dimorphism with males being larger than females, tending to have bigger white neck patches and pinker breast, although there is substantial overlap between the sexes (Baptista *et al.*, 1997; Gibbs *et al*., 2001; Huallacháin and Dunne, 2010). Breeding season varies with zone, ranging from late February to early September. Sexual maturity is reached at one year of age (Murton, 1966).

The woodpigeon characteristically resides in deciduous or coniferous forests, but can also be found in urbanized areas, sometimes causing damages to crops, reason why they are often considered a plague. This species feeds mainly on plant matter, including green leaves, seeds, buds, flowers, berries and root crops, sporadically eating invertebrates such as earthworms and beetles. Due to its largely granivorous diet, it must be noted the importance of the woodpigeon in the dissemination of seeds (Inglis *et al.*, 1990; Baptista *et al.,* 1997; Gibbs *et al.,* 2001; Dickens and Neves, 2005).

Regarding migratory behaviour, populations of woodpigeon that reproduce in Southwest and Central Europe and in some places in Northern Africa and Western Asia are resident or partially migratory, while populations in Eastern Europe and Fennoscandia are fully migratory. These latter, during the autumn-winter migrate to

southern Europe and North Africa (Gibbs *et al.,* 2001; Bea *et al.*, 2003; Höfle *et al.*, 2004).

The wide distribution of this species led to the evolution of different subspecies which display slight differences in size and colouration (Figure 1) (Baptista *et al.*, 1997; Gibbs et al., 2001). One of these subspecies is the Azorean woodpigeon (*C. p. azorica*, Hartert and Ogilvie-Grant, 1905), which is found only in the Azores archipelago (Portugal) and where it is presumed to be sedentary and breeding in all islands of the archipelago. As with other aspects of its biology, the evolutionary history of the Azorean woodpigeon has received little attention, with the exception of the efforts of Dourado et al. (2014). These authors used a combination of mitochondrial (cytochrome b and cytochrome C oxidase I) and nuclear markers (beta-fibrinogen intron 7) to understand the evolutionary history of the several endemic pigeon of the Macaronesia. With regards to the Azorean woodpigeon, they found no evidence of a phylogenetic distinctiveness to continental European population, although by their own admission this merits further investigation with a larger set of genetic markers. Even though an apparent smaller size (wing length used as proxy of size) in *C. p. azorica* has been reported, colour was the main trait used to differentiate it from the continental European *C. p. palumbus*. According to Hartert and Ogilvie-Grant (1905), the plumage of the Azorean subspecies is darker, especially in males, in several regions of the body, namely: crown, upperback, lowerback, uppertail coverts, undertail coverts, underwing coverts and a darker and more vinous tone in the chest, as well as smaller neck patches than those of *C. p. palumbus.*

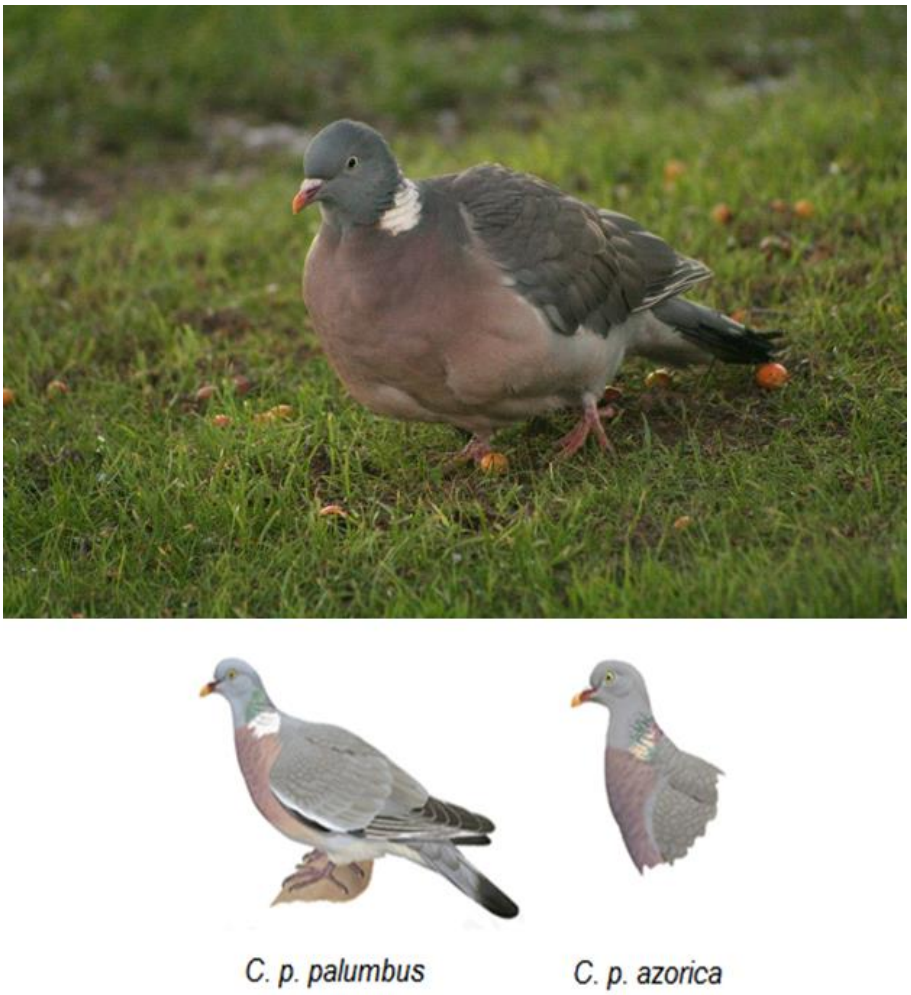

Figure 1- Woodpigeon (*Columba palumbus*), photo by Tiago Rodrigues (CIBIO-InBIO) and subspecies of woodpigeon (adapted from Baptista *et al.*, 1997).

With regard to conservation, *C. p. azorica* was a game bird until 1993, but since then it became protected by the Birds Directive. Nevertheless local farmers dislike them, because of the presumed damages they cause to the crops, and one of their biggest threats is illegal hunting as well as the replacement of natural forest areas by pasture extents (Gibbs et al., 2001; Dickens and Neves, 2005). Given this fact, the almost complete lack of knowledge about the Azorean woodpigeon, the fact that there is a big pressure to turn it into a game subspecies and doubts about its endemic subspecies taxonomic status it is important to gather information about its ecology, biology and evolution. Thus, this work follows the AZORPI project (M2.1.2/I/025/2011), funded by the Azorean regional government (through the Direção Regional do Ambiente and Direção Regional da Ciência e Tecnologia), and whose goal was to study the evolution and ecology of the Azorean woodpigeon.

As previously stated, several phenotypic differences are usually perceptible between insular and continental individuals. Regarding differences in the particular case of columbids, without clear sexual dichromatism, males still tend to show more brightness than females (Mahler and Kempenaers, 2002; Valdez and Benitez-Vieyra, 2016), which is congruent with other studies that show that female birds usually choose males with the brightest plumage (Hill, 1993; Siitari *et al.*, 2002; Jawor and Breitwisch, 2003). Some studies also show that male columbids display higher UV reflectance than females in body parts exhibited during courtship, which may indicate that those body regions are subject to sexual selection, for greater sexual dichromatism, even when there are no perceptible differences to the human eye (Mahler and Kempenaers, 2002).

Studies focusing on other species of columbiforms with regard to the effects of the isolation in insular systems in the shape and size of the body demonstrated that island columbiforms display morphological differences to their continent counterparts, generally with insular forms displaying smaller flight apparatuses, more robust bills and larger body sizes than the continental ones (Livezey, 1993; Millener and Powlesland, 2001; Worthy and Wragg, 2008; Monceau *et al.*, 2013). Millener and Powlesland (2001) also showed that the Chatham pigeon (*Hemiphaga chathamensis* Rothschild, 1891) has larger feet than populations from mainland and those from the smaller and more isolated islands have relative bigger feet, suggesting an adaptation to sedentarisation, spending more time in the ground and less adapted for long sustained flight.

1.4 – Objectives

The main goal of this study was to identify phenotypic differences (both in colouration and morphology) between insular and continental populations of the woodpigeon. Differences in the shape and size of the feeding and locomotor apparatuses as well as in the colour between the two subspecies were tested since different selective pressures are expected to have been felt by populations in the Azores, related to differences in habitat, use of resources and migratory behaviour and other life-history traits. Differences between sexes, both in morphology and colour, were also tested, as islands harbour conditions for shifts in sexual selection intensity to occur (for example, higher population densities and thus possible increase in competition for mates). Apart from increasing basic knowledge on the evolution of insular populations of the woodpigeon, this work aims to provide updated knowledge to

be considered in future conservation planning and to understand if the Azorean subspecies can be considered an endemism of the archipelago.

2- Material and methods

2.1- Sampling

The woodpigeon specimens used in this study were mostly collected by hunting (in the case of the protected Azorean subspecies authorization was given by the Direção Regional do Ambiente, license number 59/2013/DRA) while others were found dead, usually as a result of road kills. The Azorean sample was composed of individuals from seven islands of the Azores archipelago (Figure 2): Faial, Graciosa, Pico, S. Jorge and Terceira from the Central Group; Santa Maria and S. Miguel from the Eastern Group; no specimens from the Western Group were collected, as the species is rare in these islands. From continental Europe woodpigeon specimens were obtained from Portugal, Spain, France and Denmark (Figure 2). The sample size from each location used for morphology and spectrophotometry analysis was slightly different (Table 1). Details about each specimen used (sex, subspecies, sample sites and approximate coordinates) are presented in Table A1 in appendix.

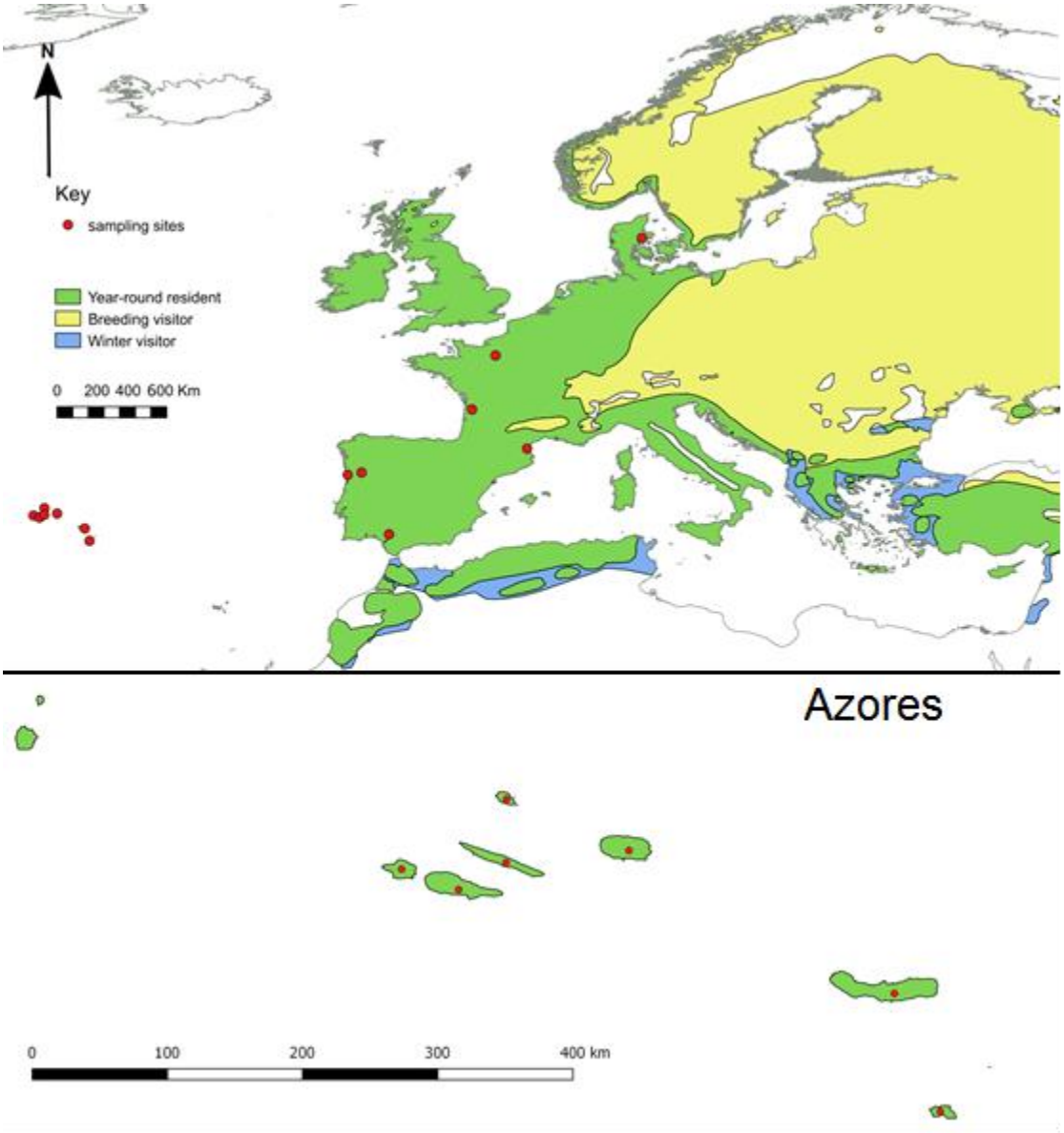

Figure 2- Woodpigeon's (*Columba palumbus*) breeding (yellow), all year-round (green) and wintering (blue) ranges (adapted from Baptista *et al.*, 1997). Red dots indicate the regions where the birds were collected (Azores Eastern Group and Central Group, continental Portugal (Porto and Vila Real), Spain (Seville), France (Charente-Maritime, Eure and Ortaffa) and Denmark (Aarhus). Woodpigeon distribution map was obtained from BirdLife International and NatureServe (2015).

Table 1 - Sample size (number of individuals) from each location used for morphology and spectrophotometry analysis.

Analysis	Azores		Europe				Total
	Central Group	Eastern Group	Portugal	Spain	France	Denmark	
Spectrophotometry	57	20	22	13	9	12	133
Morphology	57	20	13	12	7	11	120

2.2- Spectrophotometric data collection

In order to quantify woodpigeons' colouration in plumage patches previously suggested to have diverged between Azorean and continental European specimens, as well as potentially being implicated in sexual dimorphism, light reflectance values were measured using an Ocean Optics USB 4000 reflection spectrophotometer coupled to a pulsed Xenon light source, allowing an objective analysis of colour. The measurements were taken with a probe, being calibrated between each measured bird with a white certified reflectance standard and a black velvet cloth used as a black reference standard. A black rubber mounted on the end of the probe kept it at a fixed distance from the feathers, and helped avoid contamination from sunlight. Birds from the Azores and continental Europe were measured alternately. All the measurements were taken by the same person (Daniele Cataldo). Measurements were taken in 37 points distributed across 9 different body regions (Figure 3): four in the crown, three in the upperback, three in the lowerback, four in the uppertail coverts, four in the undertail coverts, four in the underwing coverts and fifteen along the chest divided in three sections: throat, upper chest and lower chest with five measurements each section. In some birds the condition of the plumage did not allow to take every measurement. To take this into account only the patches with at least two points measured were taken into consideration, since the average spectra from different points on a patch, rather than taking a single measurement, allows to account for colour heterogeneity (Cardoso and Gomes, 2015). Only birds with adult plumage (i.e. after their first post-juvenile moult) were considered. Then, for each bird, the mean value of the reflectance was calculated for each body region with reflectance data trimmed to the interval between 300 and 700 nm, corresponding to the avian visual spectra as previously stated. Spline interpolation, using the spline program from GNU plotutils 2.6 (Maier, 2009) on the original data was used for curve smoothing, sampling 100 values from the newly generated curve. Throat was not used in statistical analysis due to the large number of missing data in this area.

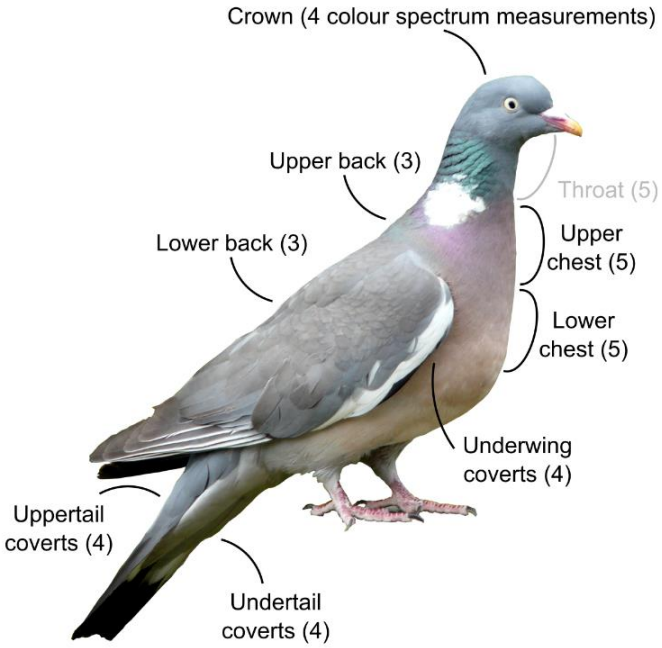

Figure 3- Body regions where measurements were taken. Measurements were taken in 37 points distributed across 9 different body regions: four in the crown (points 1 to 4), three in the upperback (5 to 7), three in the lowerback (8 to 10), four in the uppertail coverts (11 to 14), four in the undertail coverts (15 to 18), four in the underwing coverts (19 to 22) and fifteen along the chest divided in three sections: throat (23 to 27), upper chest (28 to 32) and lower chest (33 to 37).

Then, some classic colourimetric variables were calculated according to Hill and McGraw (2006), for each individual for each plumage patch: total brightness (sum of all the reflectances of the whole spectrum considered, 300-700 nm), intensity (maximum reflectance in the spectrum considered), red, blue and UV chromas (ratio of the sum of the reflectances of an interval by the sum of the reflectances of the whole spectrum considered) and spectral saturation (ratio of the maximum reflectance by the minimum reflectance in the spectrum considered) (Table A2 in Appendix).

2.3- Morphometric data collection

In order to understand if the Azorean subspecies is morphologically different from the continental European subspecies and there are differences among sexes, external and internal (skeletal) measurements (Figures 4 and 5) were taken and analysed.

External morphometric information (linear measurements) of several functional complexes of the individuals was collected (Figure 4; following Eck *et al.*, 2011) head and feeding apparatus (head length, bill to skull length, bill to cere length, bill depth and bill width, with a digital calliper, ±0.01 mm), flight apparatus (wing length, alula length,

tail length, length of the primary feathers and the first secondary feather, with rulers, ±0.5 mm) and locomotor apparatus (tarsus length, tarsus depth, tarsus height, foot span and lengths of the hind, inner, central and outer toes, with a digital calliper, ±0.01 mm). Very worn or growing feathers were ignored. Measurements were collected preferentially on the right side of the bird except when the preservation status of the specimen did not allow it, noting if the measurement was made on the left side. All external measurements (Figure 4) were taken by the same person (Pedro Andrade; CIBIO-InBIO).

For skeleton preparation a modified procedure from that described by Davis and Payne (1992) and Baker *et al.* (2003) was used. First, the specimens were dissected and feathers, skin, viscera and muscle were removed. During this process gonads and the presence/absence of the bursa of Fabricius was inspected in order to assess, respectively, the sex and confirm if the individuals were juveniles. Due to the poor preservation condition of some of the individuals, the gonads could not be analysed so molecular sexing using the P2/P8 primer pair in polymerase chain reaction was used in these instances (Griffiths *et al.*, 1998). After defleshing, specimens were put into nylon mesh bags and went to simmering water from ten to fifteen minutes, bringing it to near boiling point, softening the flesh, ligaments and tendons without weakening the bones and, consequently, speeding the following enzymatic process significantly. Afterwards, specimens were placed and kept in a bucket filled with tap water and household detergent (Ariel®, 10 mL/L) containing a proteolytic enzyme, during approximately 7 days at 45 °C to digest the rest of the flesh. After the enzymatic treatment the bones of each specimen were manually cleaned. Carcasses were degreased through a sequence of jars containing increasingly cleaner acetone for about two weeks. Then, the bones were left in a container in order to dry and then placed in plastic bags and stored.

Several linear measurements were taken (nomenclature from von den Driesch, 1976) (Figure 5) from:

- Cranium and feeding apparatus: greatest length of the cranium (GL), bill length, cranium height, cranium width and mandible length;
- Pectoral girdle: sternum length, keel crista and keel depth, coracoid greatest length (GL), coracoid basal breadth (Bb) and coracoid distal breath (Db) and furcula length;
- Fore limb: humerus and radius greatest length (GL), smallest breadth of the corpus (SC), breadth of the distal epiphysis (Bd) and breadth of the proximal epiphysis (Bp); ulna greatest length (GL), smallest breadth of the corpus (SC), breadth of the proximal epiphysis (Bp) and diagonal of the distal epiphysis (Did)

and carpometacarpus breadth of the proximal epiphysis (Bp), greatest length (GL) and diagonal of the distal epiphysis (Did).

- Pelvis: pelvis length and ischium depth;
- Hind limb: femur and tarsometatarsus greatest length (GL), smallest breadth of the corpus (SC), breadth of the distal epiphysis (Bd) and breadth of the proximal epiphysis (Bp) and tibiotarsus greatest length (GL), smallest breadth of the corpus (SC), breadth of the distal epiphysis (Bd) and diagonal of the proximal epiphysis (Dip);

All the bones were measured by the same person (Daniele Cataldo) using a digital calliper with a precision of 0.01 mm. It is important to note that some structures and bones were broken or missing so the database had some missing data. Juvenile specimens (i.e. collected during their first calendar year) were not taken into consideration in further analyses as many of them had not yet completed body growth.

Since measurements on the appendicular skeleton were taken on both left and right bones, this was used to compensate for missing values in the database when no significant asymmetry was verified. Briefly, for each left/right bone combination, a non-parametric two-sample paired test (Wilcoxon signed-rank test) was used to test for consistent significant differences between the left and right bone. In variables that did not show significant differences ($p<0.05$) between both sides, measurements were used interchangeably to complement blank spaces in the dataset. Significant differences were found for four variables (Tarsometatarsus Bd, carpometacarpus Bp, carpometacarpus Did and tibiotarsus GL; Figure 5), so in these cases values were not exchanged and the most complete side for each one of them was used in further analyses.

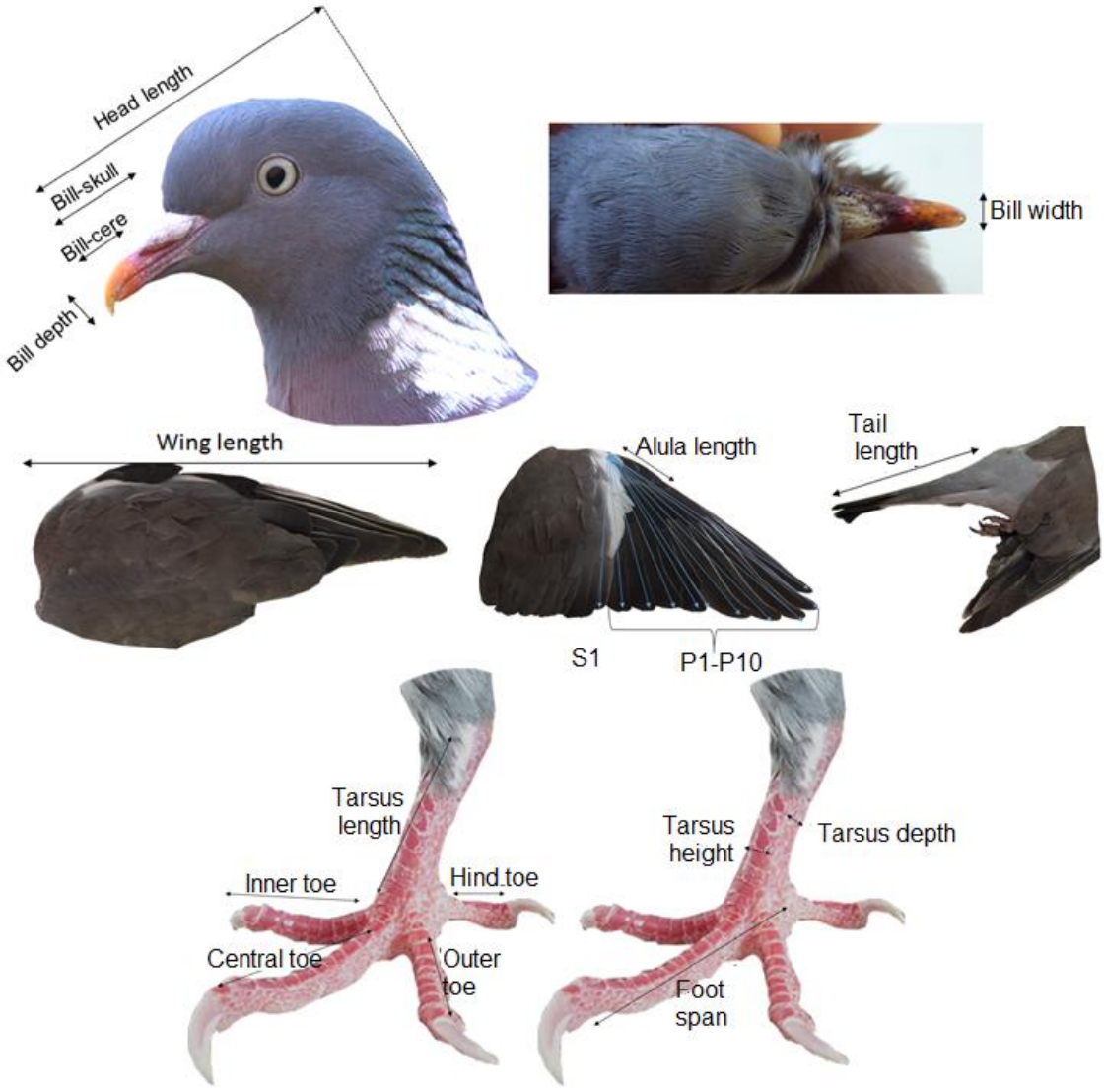

Figure 4- External measurements taken from the head and feeding apparatus, tail, wing, foot and leg. Primaries (P1 to P10) are numbered from body toward the wing tip.

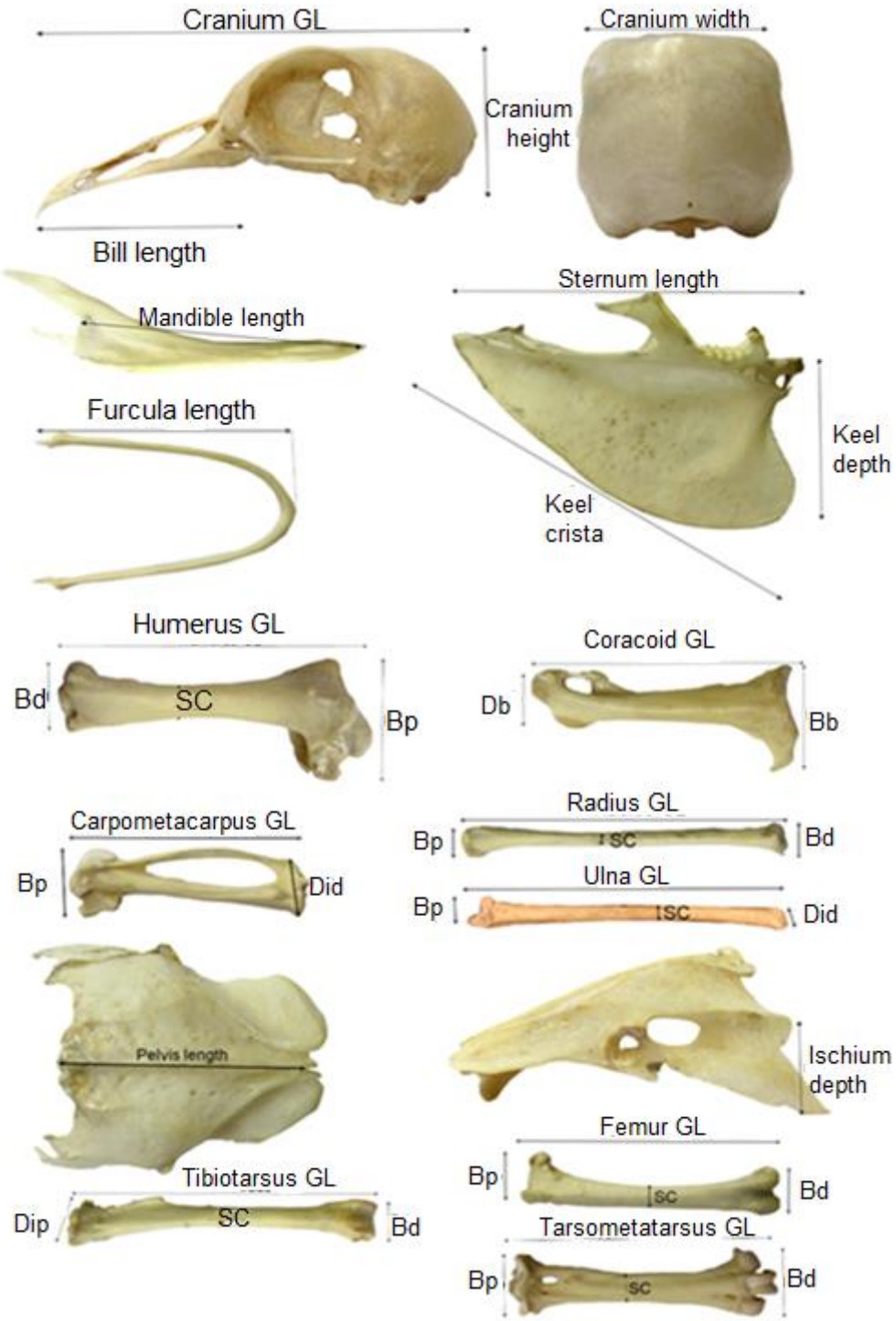

Figure 5- Skeletal measurements taken from the cranium, mandible, sternum, furcula, coracoid, humerus, radius, ulna, carpometacarpus, pelvis, femur, tibiotarsus and tarsometatarsus.

2.4- Spectrophotometric and morphometric data analysis

Data analysis from both plumage colour and morphological data was conducted in a similar manner (using the software PAST v.3.15, Hammer *et al.*, 2001). Univariate outliers in the morphology dataset were removed using Tukey's method, while for the spectrophotometry dataset multivariate outliers were removed using multivariate Mahalanobis distances (to account for the fact that all variables were calculated from the same curve). Normality for each variable was tested using Shapiro-Wilk's tests. For those that showed significant deviations from normality ($p<0.05$), the distribution was inspected graphically and no extreme deviations from normality were observed. Still, distribution-free non-parametric tests were used in further analyses.

To test for variance homogeneity (homoscedasticity), Levene´s test was used considering four groups (Azorean females, Azorean males, Continental females and Continental males). For the few variables that violated the assumption of homogeneity of variance (at $p<0.05$), subsampling of each group to the sample size of the group with the least amount of measured individuals was done to diminish inter-group variance heterogeneity in subsequent analyses. To test for differences among populations and sexes, as well as possible interactions (which could indicate possible shifts in the intensity of sexual selection between geographical locations), non-parametric two-way permutational analysis of variance (PERMANOVA) with geographical provenance (Azores or Continental Europe) and sex (males or females) as factors were used to compare differences in each spectrophotometric and morphological variable measurement (univariate analysis).

In order to condense the data into summarized variables, principal component analysis (PCA) on correlation matrices was used since it takes into consideration all the variable's dimensions, turning them into orthogonal principal components, facilitating their interpretation (Chandler and Mulvihill, 1988). To account for missing data in the sample, PCA with an iterative model to calculate missing data were performed (Ilin and Raiko, 2010). For each analysis, a missing data threshold of 20% was set, so individuals that had more than 20% of missing measurements in each analysis were eliminated to avoid inaccurate estimates of principal component values (Brown *et al.*, 2012). Before conducting PCA, multivariate outliers were removed to prevent components being dominated by extreme values. The analyses conducted were as follows:

Spectrophotometry:

Two PCA were performed, one with all measurements of brightness and intensity (*BrightnessPCA*) and another considering all measurements of red chroma, blue chroma, UV chroma and spectral saturation (*ColourPCA*).

Morphology:

A PCA (*BodysizePCA*) with the greatest lengths of the cranium, sternum, pelvis, femur, tibiotarsus, radius and carpometacarpus was performed. Then, all the original variables were corrected for size in order to remove allometric effects (the PC1 value was used as a correction factor, according to Lleonart *et al.*, 2000). Then, five PCA were performed, a *HeadPCA* with external and skeletal measurements of the head combined since some structures are easier to collect on the outside such as the bill to cere length, a *WingbonePCA* with skeletal measurements of the wing, a *WingexternalPCA* with wing feather measurements, a *PectoralPCA* with bone measurements of the coracoid, furcula and sternum and a *LegPCA* with both external and skeletal measurements combined since some measures are easier to collect on the outside (e.g. measures associated with fingers).

Next, individual scores were used as variables in subsequent two-way PERMANOVA, following the same procedure as described above (geographical provenance and sex as factors).

3- Results

3.1- Spectrophotometry results

Univariate analysis

The two-way PERMANOVA tests showed the occurrence of several colour differences between insular and continental subspecies of woodpigeon as well as differences between males and females (Table 2). No differences between sex and subspecies were observed in the undertail coverts with regard to the univariate analysis.

Univariate analyses of brightness and intensity show that the continental subspecies is brighter than the insular one in the majority of the body regions, except in the undertail coverts where no differences were observed (Table 2). Regarding brightness, lower chest was the only body part with differences between sexes (females being brighter than males). These patterns are also perceptible in the mean reflectance graphic representation (Figure 6).

Table 2- Results of non-parametric two-way PERMANOVA to test the occurrence of significant differences in spectrophotometric univariate variables for different sex (Male- M/ Female- F) and subspecies (Continental- C/ Azores- A) of woodpigeon. Only significant results ($p<0.05$) are presented.

Body part	Variable	System		Sex		Interaction		Comparison
		Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	
Crown	Total brightness	20.91	0.0001					C>A
	Intensity	13.09	0.0004					C>A
	Red chroma	9.57	0.0021	6.39	0.0112			C>A; F>M
	Blue chroma							
	UV chroma	11.47	0.0011	7.54	0.0047			A>C; M>F
	Spectral saturation	4.02	0.0368					C>A
Upperback	Total brightness	80.97	0.0001					C>A
	Intensity	75.69	0.0001					C>A
	Red chroma			9.79	0.0017			F>M
	Blue chroma	4.44	0.0312	10.23	0.0014			C>A; M>F
	UV chroma			6.56	0.0093			M>F
	Spectral saturation			7.19	0.0056			F>M
Lowerback	Total brightness	69.29	0.0001					C>A
	Intensity	51.66	0.0001					C>A
	Red chroma							
	Blue chroma	7.16	0.0081					C>A
	UV chroma							
	Spectral saturation	15.56	0.0002					C>A
Uppertail coverts	Total brightness	20.76	0.0001					C>A
	Intensity	28.26	0.0001					C>A
	Red chroma							
	Blue chroma	29.03	0.0001					C>A
	UV chroma							
	Spectral saturation	6.05	0.0122					C>A
Undertail coverts	Total brightness							
	Intensity							
	Red chroma							
	Blue chroma							
	UV chroma							
	Spectral saturation							
Underwing coverts	Total brightness	34.77	0.0001					C>A
	Intensity	29.89	0.0001					C>A
	Red chroma							
	Blue chroma	5.99	0.0139					C>A
	UV chroma							
	Spectral saturation	12.04	0.0014					C>A
Upper chest	Total brightness	19.38	0.0001					C>A
	Intensity	23.66	0.0001					C>A
	Red chroma							
	Blue chroma							
	UV chroma			5.87	0.0119			M>F
	Spectral saturation	4.18	0.035	3.63	0.0484			F>M; C>A
Lower chest	Total brightness	18.20	0.0001	25.36	0.0001			C>A; F>M
	Intensity	10.66	0.0019	19.49	0.0001			C>A; F>M
	Red chroma	7.88	0.005					A>C
	Blue chroma	15.55	0.0002	6.57	0.0104			C>A; F>M
	UV chroma			4.74	0.0291			M>F
	Spectral saturation							

Univariate analyses of colour indicate that insular woodpigeon shows higher UV chroma values than the continental woodpigeon in the crown, while the later show higher red chroma values in that area. However, insular birds show higher red chroma in lower chest than the continental ones. Continental birds are the ones with higher blue chroma values in the upperback, lowerback, uppertail coverts, underwing coverts and lower chest and higher spectral saturation in the crown, lowerback, uppertail coverts, underwing coverts and upper chest.

Regarding differences between sexes, males show higher UV chroma values than females in the crown, upperback, upper chest and lower chest while females show higher red chroma values than males in the crown, upperback and upper chest and higher spectral saturation than males in the upperback. Regarding blue chroma, females show higher values in lower chest while males show higher values than females in the upperback.

Multivariate analysis

In order to evaluate overall coloration patterns two PCA were performed, as previously described recovering the components presented in Tables 3 and 4.

Concerning colour, the first principal component (*ColourPC1*) explains 34.0% of the variance and shows a UV versus Red chroma pattern (Table 3). The second principal component (*ColourPC2*) explains 14.3% of the variance and is consistently positively correlated with all blue variables (Table 3) so it can be translated as an index of blueness.

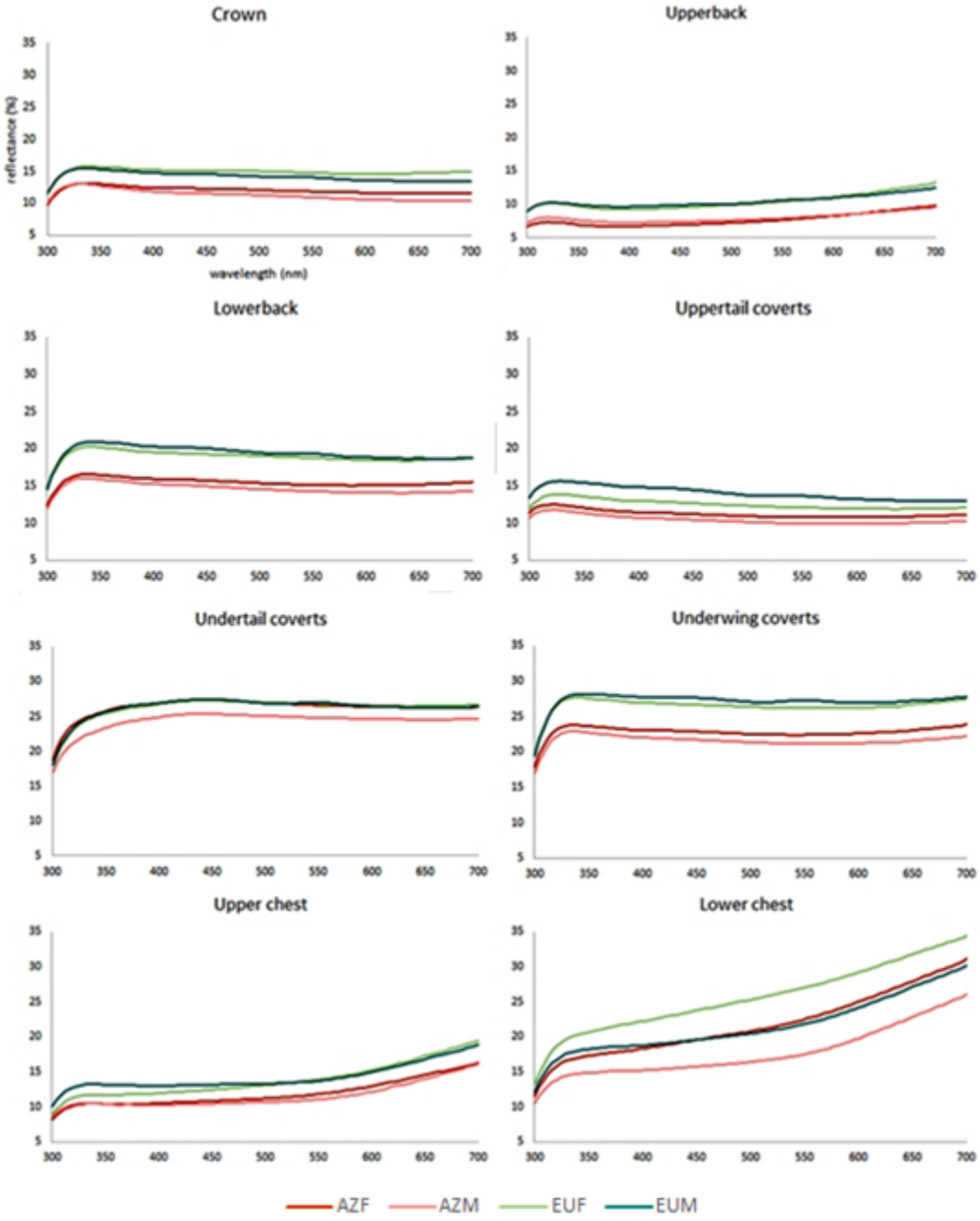

Figure 6- Mean reflectance for Azorean and Continental birds in eight plumage patches: crown; upperback; lower back; uppertail coverts; undertail coverts; underwing coverts; upper chest and lower chest. Values for female Azorean birds (AZF) are in brown, male Azorean birds (AZM) in pink, while the ones for female European continental birds (EUF) are in green and male European continental birds (EUM) are in blue.

Table 3- Principal component analysis of colour (*ColourPCA*) from the woodpigeon (*Columba palumbus*). Significant (p<0.05) correlations between variables and the principal components are signalled in bold.

	ColourPC1	*ColourPC2*
Crown - RED chroma	**0.181**	0.086
Upperback - RED chroma	**0.241**	-0.093
Lowerback - RED chroma	**0.202**	-0.067
Uppertail - RED chroma	**0.172**	-0.087
Undertail - RED chroma	**0.190**	0.064
Underwing - RED chroma	**0.226**	0.042
Upper chest - RED chroma	**0.205**	**-0.178**
Lower chest - RED chroma	0.070	**-0.327**
Crown - BLUE chroma	0.025	**0.154**
Upperback - BLUE chroma	-0.147	**0.259**
Lowerback - BLUE chroma	-0.002	**0.282**
Uppertail - BLUE chroma	0.024	**0.278**
Undertail - BLUE chroma	0.108	**0.193**
Underwing - BLUE chroma	-0.040	**0.258**
Upper chest - BLUE chroma	-0.104	**0.283**
Lower chest - BLUE chroma	0.024	**0.367**
Crown - UV chroma	**-0.213**	**-0.158**
Upperback - UV chroma	**-0.264**	-0.030
Lowerback - UV chroma	**-0.240**	-0.092
Uppertail - UV chroma	**-0.221**	-0.092
Undertail - UV chroma	**-0.195**	-0.112
Underwing - UV chroma	**-0.222**	**-0.181**
Upper chest - UV chroma	**-0.250**	0.059
Lower chest - UV chroma	**-0.211**	**0.220**
Crown - Spectral saturation	0.085	0.035
Upperback - Spectral saturation	**0.249**	-0.041
Lowerback - Spectral saturation	**0.173**	**0.169**
Uppertail - Spectral saturation	-0.084	-0.095
Undertail - Spectral saturation	**0.188**	0.140
Underwing - Spectral saturation	0.136	0.120
Upper chest - Spectral saturation	**0.232**	-0.049
Lower chest - Spectral saturation	**0.167**	**-0.208**
Eigenvalue	10.882	4.567
% of total variance	34.005	14.273
n=81		

The analysis of brightness gave a first principal component (*BrightnessPC1*) that explains 54.3% of the variance and increases in this component reflect increases in overall brightness (Table 4). The second principal component (*BrightnessPC2*) explains 12.0% of the variance and is correlated with inverse variation of the tail coverts versus the variation in the upper chest.

Table 4- Principal component analysis of brightness (*BrightnessPCA*) from the woodpigeon (*Columba palumbus*). Significant (p<0.05) correlations between variables and the principal components are signalled in bold.

	BrightnessPC1	*BrightnessPC2*
Crown – total brightness	**0.246**	-0.102
Upperback – total brightness	**0.280**	-0.123
Lowerback – total brightness	**0.298**	-0.035
Uppertail – total brightness	**0.242**	**0.213**
Undertail – total brightness	**0.187**	**0.536**
Underwing – total brightness	**0.302**	0.027
Upper chest – total brightness	**0.219**	**-0.365**
Lower chest – total brightness	**0.231**	-0.044
Crown – intensity	**0.238**	-0.078
Upperback – intensity	**0.253**	-0.167
Lowerback – intensity	**0.295**	-0.029
Uppertail – intensity	**0.244**	**0.202**
Undertail – intensity	**0.194**	**0.527**
Underwing – intensity	**0.302**	0.014
Upper chest – intensity	**0.199**	**-0.388**
Lower chest – intensity	**0.224**	-0.041
Eigenvalue	8.692	1.918
% of total variance	54.326	11.985
n= 83		

Concerning colour, according to *ColourPC1*, females display higher spectral saturation and red chroma values while males show higher UV chroma values (Table 5). Regarding this component, there was an interaction (Table 5), which occurs due to a stronger difference in this component between males and female in the continent (Figure 7). Regarding *ColourPC2* there is a pattern of intense blue chroma in continental birds and less blueness in insular birds (Table 5).

Regarding *BrightnessPC1,* continental individuals are brighter (present higher values of this component) than the insular subspecies (Table 5). The second principal component (*BrightnessPC2*) analysis indicates that continental birds are brighter in the chest and darker in the tail and the insular subspecies with brighter tail and darker chest (Table 5). This way, while comparing both populations and sexes for multivariate overall brightness, *BrightnessPC1* confirms that insular subspecies is less bright than the continental European one in the overall body and continental individuals are brighter in the chest even though they have proportionally darker undertail coverts according to *BrightnessPC2*.

Table 5 - Results of non-parametric two-way PERMANOVA to test the occurrence of significant differences in multivariate indices of brightness and colour derived from principal component analysis for different sex (Male (M)/Female (F)) and subspecies (Continental (C)/Azores (A)) of woodpigeon (*Columba palumbus*). Only significant results (p<0.05) are presented.

Variable	System		Sex		Interaction		Comparison
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	
ColourPC1			4.03	0.0496	7.74	0.0073	
ColourPC2	20.04	0.0001					C>A
BrightnessPC1	44.71	0.0001					C>A
BrightnessPC2	4.61	0.0267					A>C

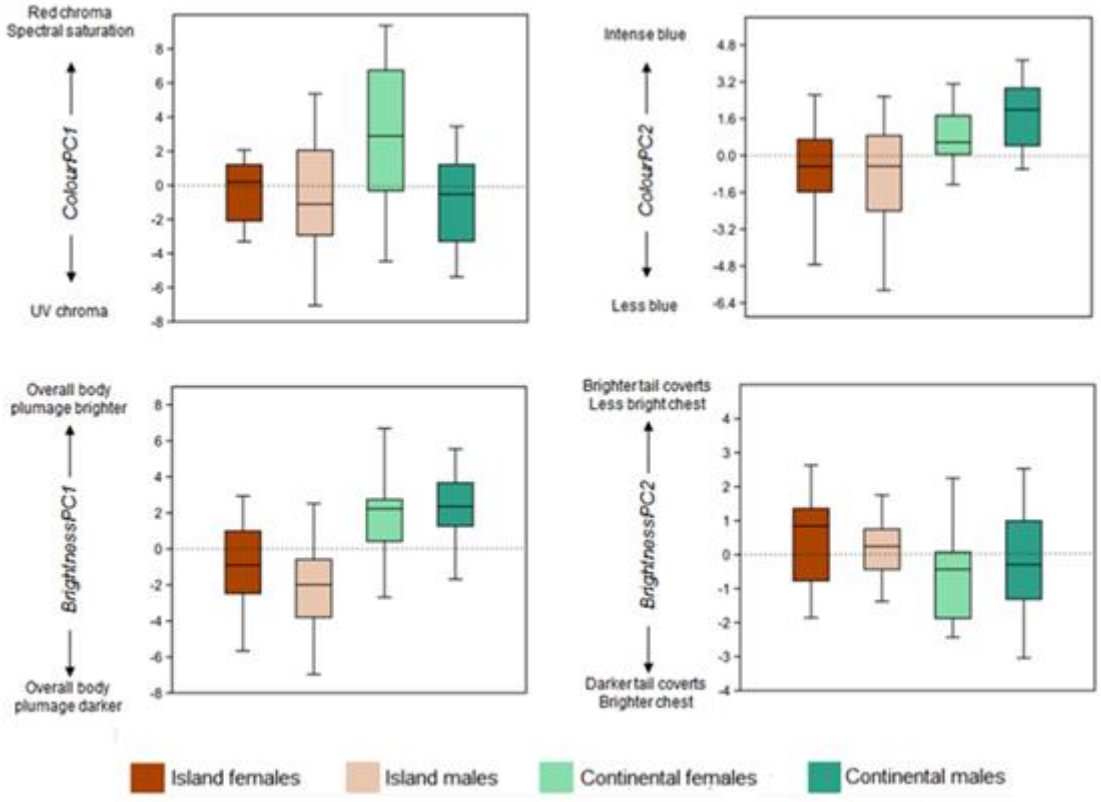

Figure 7- Differences between female and male insular birds and female and male continental birds regarding, *ColourPC1*, *ColourPC2, BrightnessPC1* and *BrightnessPC2* values

3.2- Morphometry results

Univariate analysis

Univariate analyses (Table 6) showed a consistent pattern of males being significantly bigger than females in external and skeletal measurements across most of the body. Regarding differences between subspecies, the insular woodpigeon displays

significantly bigger alula length, external and skeletal portions of the bill (bill length and width), leg (femur, tibiotarsus and tarsometatarsus measurements as well as tarsus length, foot span, inner and central toes) and pelvis (ischium depth) than the continental subspecies which in turn displays bigger cranium width, sternum (sternum length, keel depth and keel crista), furcula length and coracoid (coracoid GL, Bb and Db) as well as some primary feather (P4, P5 and P7).

Some results of the univariate analyses are harder to interpret such as bigger radius breadth of the proximal epiphysis (Radius Bp) in insular birds and bigger humerus greatest length (Humerus GL), ulna breadth of the proximal epiphysis (Ulna Bp) and humerus breadth of the proximal epiphysis (Humerus Bp) in continental birds, as well as some interactions. Therefore, PCA were performed in order to understand general patterns of body size and shape.

The detailed descriptive statistics of external and skeletal measurements of each sex for insular and continental birds are presented in Table A3 in appendix.

Table 6- Results of non-parametric two-way PERMANOVA to test the occurrence of significant differences in univariate variables for different sex (Male- M/Female- F) and subspecies (Continental- C/Azores- A) of woodpigeon. Only significant results ($p<0.05$) are presented. S1 - first secondary (the outermost); P1 to P10 - Primaries, numbered from body toward the wing tip.

Variable	System		Sex		Interaction		Comparison
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	
Wing							
Alula length	11.02	0.0012	7.45	0.0041			A>C; M>F
Tail			13.52	0.0005			M>F
Head							
Bill-skull							
Bill-cere							
Bill depth							
Bill width	7.53	0.0042					A>C
Tarsus length	4.77	0.0230	5.31	0.0160			A>C; M>F
Tarsus depth			6.99	0.0059			M>F
Tarsus height							
Foot span	10.49	0.0011					A>C
Hind toe							
Inner toe	6.85	0.0067					A>C
Central toe	10.43	0.0014					A>C
Outer toe							
Cranium GL							
Bill length	6.23	0.0100					A>C
Cranium height			5.96	0.0108			M>F
Cranium width	13.39	0.0002					C>A
Mandible length			5.60	0.0124			M>F
Sternum length	20.91	0.0001					C>A
Keel depth	49.10	0.0001					C>A
Keel crista	13.11	0.0004			-2.05	0.0158	
Furcula length	44.19	0.0001					C>A
Coracoid GL	6.83	0.0051					C>A
Coracoid Bb	14.42	0.0001	3.97	0.0373			C>A; M>F
Coracoid Db	7.28	0.0049	5.57	0.0144			C>A; M>F
Humerus GL	15.06	0.0001	16.66	0.0002	-0.49	0.0245	

Variable	System		Sex		Interaction		Comparison
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	
Humerus Bp	4.93	0.0209	4.44	0.0292	8.41	0.0010	
Humerus Bd			8.11	0.0037	7.30	0.0012	
Humerus SC							
Radius GL			12.69	0.0005			M>F
Radius Bp	6.10	0.0089					A>C
Radius Bd			5.96	0.0096	0.14	0.014	
Radius SC			3.61	0.0444			M>F
Ulna GL			10.39	0.0008			M>F
Ulna Bp	4.73	0.0209	12.90	0.0004			C>A; M>F
Ulna Did							
Ulna SC							
Carpometacarpus GL			3.95	0.0326			M>F
Carpometacarpus Bp							
Carpometacarpus Did							
Pelvis length							
Ischium depth	23.50	0.0001	4.85	0.0209			A>C; M>F
Tibiotarsus GL	15.28	0.0002	3.79	0.042			A>C; M>F
Tibiotarsus Dip	5.60	0.0132	10.88	0.0056			A>C M>F
Tibiotarsus Bd	13.32	0.0004	5.60	0.0144			A>C; M>F
Tibiotarsus SC			9.39	0.0014			M>F
Femur GL	8.35	0.0033	26.31	0.0001			A>C; M>F
Femur Bp	15.04	0.0002	14.64	0.0001			A>C M>F
Femur Bd	11.36	0.0007					A>C
Femur SC	6.30	0.0086	4.55	0.0265			A>C; M>F
Tarsometatarsus GL	7.07	0.0062	8.30	0.0018			A>C; M>F
Tarsometatarsus Bp	16.42	0.0002	5.16	0.0156			A>C; M>F
Tarsometatarsus Bd	6.33	0.0438	5.23	0.0165			A>C; M>F
Tarsometatarsus SC							
S1			12.14	0.0005			M>F
P1			16.95	0.0001			M>F
P2			23.25	0.0001			M>F
P3			20.11	0.0002			M>F
P4	12.29	0.0004	20.95	0.0001			C>A; M>F
P5	15.52	0.0001	11.00	0.0004			C>A; M>F
P6			6.99	0.0069			M>F
P7	3.41	0.0485	6.01	0.0088			C>A; M>F
P8			7.78	0.0046			M>F
P9							
P10			4.08	0.0376			M>F

Multivariate analysis

As previously stated a PCA (*BodysizePCA*) with the greatest lengths of the cranium, sternum, pelvis, femur, tibiotarsus, radius and carpometacarpus was performed (Table 7). The first component (*BodysizePC1*) corresponds to 51.9% of total variance and can be interpreted as corresponding to structural size, since all variables present a positive correlation in this component and increasing values of *BodysizePC1* indicate bigger body sizes. This way, *BodysizePC1* was used to correct the original variables for size in order to remove allometric effects. The second component

(*BodysizePC2*) corresponds to 16.8% of total variance and, as it increases, indicates bigger sternum and cranium and smaller pelvis and legs (Table 7).

Table 7 - Principal component analysis of body size (*BodysizePCA*) from the woodpigeon (*Columba palumbus*). Significant ($p<0.05$) correlations between variables and the principal components are signalled in bold.

	BodysizePC1	*BodysizePC2*
Cranium GL	**0.214**	**0.629**
Sternum length	**0.248**	**0.664**
Radius GL	**0.484**	-0.053
Carpometacarpus GL	**0.451**	-0.034
Pelvis length	**0.159**	**-0.177**
Tibiotarsus GL	**0.453**	**-0.294**
Femur GL	**0.473**	**-0.204**
Eigenvalue	3.635	1.174
% of variance	51.932	16.768
n= 101		

In order to better understand how the size and shape of the head and bill vary, a PCA (*HeadPCA*) with external and skeletal measurements (size corrected) of the bill and head was performed (Table 8). The two first components explain respectively 33.8% and 16.3% of variation observed in the data. All the measurements were positively correlated in the first component (*HeadPC1*) (Table 8), being interpreted as a component of size. The second component (*HeadPC2*) represents a shape component with bill depth, cranium height and cranium width positively correlated with it and the length of the bill (bill to skull and bill to cere lengths) negatively correlated (Table 8). Therefore, the second component can be interpreted as representing the variation in shape of the head and bill, with bills being shorter but deeper and craniums being bigger along this component (growing sense).

Table 8- Principal component analysis of both external and skeletal measurements of the head (*HeadPCA*) from the woodpigeon (*Columba palumbus*). Significant (p<0.05) correlations between variables and the principal components are signalled in bold.

	HeadPC1	*HeadPC2*
Head	**0.413**	-0.058
Bill-skull	**0.362**	**-0.218**
Bill-cere	**0.296**	**-0.333**
Bill depth	**0.181**	**0.201**
Bill width	**0.299**	0.051
Cranium GL	**0.454**	0.010
Bill length	**0.376**	-0.087
Cranium height	**0.145**	**0.604**
Cranium width	0.043	**0.623**
Mandible length	**0.343**	0.185
Eigenvalue	3.378	1.628
% of variance	33.781	16.284
n= 100		

In order to understand how the size and shape of the flight structures vary, three PCA were performed (always using size corrected variables): one with skeletal measurements of the forelimb so that internal size and shape of the wing were taken into account (*WingbonePCA*; Table 9); another with wing feather measurements (*WingexternalPCA*; Table 10) and a third with measurements of the pectoral girdle (furcula, coracoid and sternum), so that pectoral muscle development was indirectly analysed (*PectoralPCA*; Table 11).

The analysis of the *WingbonePCA* resulted in a first component (*WingbonePC1*) that explains 33.8% of the variance and can be interpreted as the overall increase in size of the wing, since all variables are positively correlated (Table 9). The second component (*WingbonePC2*) explains 12.6% of the variance and indicates an index of shape with lower values of length and higher values of breadth of the bones along the gradient.

Table 9- Principal component analysis of skeletal measurements of the wing (*WingbonePCA*) from the woodpigeon (Columba palumbus). Significant (p<0.05) correlations between variables and the principal components are signalled in bold.

	WingbonePC 1	*WingbonePC 2*
Humerus GL	**0.317**	**-0.308**
Humerus Bp	**0.278**	-0.023
Humerus Bd	**0.317**	0.143
Humerus SC	**0.258**	**0.166**
Radius GL	**0.313**	**-0.347**
Radius Bp	**0.165**	**0.324**
Radius Bd	**0.255**	**0.169**
Radius SC	**0.219**	**0.250**
Ulna GL	**0.300**	**-0.444**
Ulna Bp	**0.341**	0.112
Ulna Did	**0.210**	**0.175**
Ulna SC	**0.176**	**0.205**
Carpometacarpus GL	**0.272**	**-0.338**
Carpometacarpus Bp	**0.188**	**0.203**
Carpometacarpus Did	**0.154**	**0.320**
Eigenvalue	5.072	1.89
% of variance	33.813	12.599
n= 100		

Relatively to the wing feather analysis (*WingexternalPCA*), the first component (*WingexternalPC1*) corresponds to 66.6% of the total variance and can be considered as representing an overall increase in the size of the wing, because all variables have a positive correlation with this component (Table 10). As for the second component (*WingexternalPC2*), which explains 8.76% of the variance, it is associated with differences in wing shape, specifically wing pointedness, as outer wing feathers (P7 to P10) are positively correlated with this component and inner feathers (S1 to P6) negatively correlated.

Table 10- Principal component analysis of feathers of the wing, (*WingexternalPCA*) from the woodpigeon (Columba palumbus). Significant (p<0.05) correlations between variables and the principal components are signalled in bold. S1 - first secondary (the outermost); P1 to P10 - Primaries, numbered from body toward the wing tip.

	WingexternalPC1	*WingexternalPC2*
S1	**0.259**	**-0.391**
P1	**0.322**	**-0.165**
P2	**0.333**	**-0.178**
P3	**0.340**	**-0.124**
P4	**0.321**	**-0.239**
P5	**0.322**	**-0.184**
P6	**0.290**	-0.089
P7	**0.304**	**0.207**
P8	**0.311**	**0.329**
P9	**0.248**	**0.491**
P10	**0.246**	**0.531**
Eigenvalue	7.331	0.963
% of variance	66.646	8.758
n= 101		

The analysis of the *PectoralPCA* resulted in a first component (*PectoralPC1*) that explains 51.6% of the total variance and is related to an overall increase in the size of the pectoral girdle (Table 11). The second component (*PectoralPC2*), which explains 12.0% of the variance, it is associated with differences in shape, with sternum measurements being negatively correlated and furcula and coracoid measurements positively correlated.

Table 11- Principal component analysis of the pectoral girdle, (*PectoralPCA*) from the woodpigeon (Columba palumbus). Significant (p<0.05) correlations between variables and the principal components are signalled in bold.

	PectoralPC1	*PectoralPC2*
Sternum length	**0.411**	**-0.519**
Keel depth	**0.448**	-0.073
Keel crista	**0.439**	**-0.389**
Furcula length	**0.307**	**0.324**
Coracoid GL	**0.355**	**0.198**
Coracoid Bb	**0.381**	**0.214**
Coracoid Db	**0.267**	**0.620**
Eigenvalue	3.615	0.838
% of variance	51.643	11.978
n= 101		

In order to assess how the size and shape of the leg and foot vary, a PCA (*LegPCA*) was performed with both external and skeletal measurements (size corrected) combined, since some measures are easier to collect on the outside (e.g.

measures associated with fingers) and according to the preliminary statistical analyses, PCA with external and internal measurements showed the same patterns (Table 12). The first component (*LegPC1*) explains 28.3% of total variation while the second component (*LegPC2*) explains 10.5%. All variables were positively correlated with *LegPC1* which is interpreted as a component of size. The second component (*LegPC2*) was interpreted as a component of shape with foot span, toes and size of the tarsus (tarsus length and tarsometatarsus GL) positively correlated versus the reverse for the width of the bones, which can be translated into bigger feet and tarsi and thinner bones.

Table 12- Principal component analysis of both external and skeletal measurements of the leg (*LegPCA*) from the woodpigeon (*Columba palumbus*). Significant ($p<0.05$) correlations between variables and the principal components are signalled in bold.

	LegPC1	*LegPC2*
Tibiotarsus GL	**0.258**	0.046
Tibiotarsus Dip	**0.242**	**-0.326**
Tibiotarsus Bd	**0.253**	**-0.147**
Tibiotarsus SC	**0.234**	**-0.270**
Femur GL	**0.278**	0.068
Femur Bp	**0.301**	**-0.120**
Femur Bd	**0.269**	**-0.195**
Femur SC	**0.274**	-0.094
Tarsometatarsus GL	**0.296**	**0.174**
Tarsometatarsus Bp	**0.287**	-0.056
Tarsometatarsus Bd	**0.255**	**-0.141**
Tarsometatarsus SC	**0.106**	**-0.302**
Tarsus length	**0.232**	**0.258**
Tarsus depth	**0.102**	0.031
Tarsus height	0.052	-0.075
Foot span	**0.247**	**0.290**
Hind toe	0.046	**0.111**
Inner toe	**0.117**	**0.413**
Central toe	**0.186**	**0.409**
Outer toe	**0.123**	**0.281**
Eigenvalue	5.658	2.100
% of variance	28.291	10.504
n= 100		

BodysizePC1, indicating overall body size, shows significant differences between sexes, but not between subspecies, with males being larger than females (Table 13), being congruent and reinforcing what was observed in the univariate comparison. On the other hand, *BodysizePC2* shows significant differences with

continental birds showing big sterna and craniums, and smaller pelvis and legs (Table 13), something that will be examined in more detail in the other PCs.

Regarding the comparison of the head and bill size component, *HeadPC1* shows no significant differences between sexes or subspecies but differences in the second component (*HeadPC2*), which corresponds to the shape of the bill and head, were significant between sexes and subspecies (Table 13). This suggests that males have shorter but deeper bills as well as bigger craniums. These results are congruent with the univariate analysis that showed males to have higher craniums. Insular birds show longer bills, being this congruent with univariate comparison, with insular populations displaying bigger bills. Continental birds also show bigger craniums, being in accordance with the univariate analyses that show continental birds to have wider craniums.

As previously stated, some results of the univariate analysis were not clear, particularly in the wing bones. When multivariate comparisons of the wing bones between subspecies and sexes was performed, males showed bigger overall size of the wing (*wingbonePC1*) than females and continental birds also had bigger wings than the insular subspecies (Table 13). However, an interaction was observed (Figure 9), meaning that differences between sexes were more pronounced in the continent than in the Azores, reinforcing the idea that these structures are more adequate to long-term flights. *WingbonePC2* showed no differences between subspecies or sexes (Table 13).

With regard to wing feathers analysis, or external wing analysis, the size component (*WingexternalPC1*) shows that the feathers of the male birds are bigger than those of females and the continental subspecies shows bigger feathers than the insular woodpigeon and thus bigger wings (Table 13). This is congruent with the univariates analysis results. The wing pointedness component (*WingexternalPC2*) is significantly different between females and males with females displaying more pointed wings (Table 13). No differences between subspecies were discernible in this component and since the percentage of variance of this component is less than 10%, the results should be viewed with caution.

PectoralPC1 shows that continental birds have bigger pectoral girdle than the insular ones (Table 13). However, an interaction was observed (Figure 8), meaning that differences between sexes were more pronounced in the continent than in the Azores like the case of *WingbonePC1* reinforcing the idea that structures linked to flight (wings and pectoral girdle) are more suitable to long-term flight in the continental birds.

Comparisons of leg size (*LegPC1*; Table 13) show that males have bigger feet and legs than females and continental birds display smaller leg size than the insular

ones, being in accordance with the results from the univariate analysis. The second component (*LegPC2*) showed no differences between sexes or subspecies.

Table 13- Results of non-parametric two-way PERMANOVA to test the occurrence of significant differences in multivariate indices of size and shape derived from previous principal component analysis for different sex (Male- M/Female- F) and subspecies (Continental- C/Azores- A) of woodpigeon (*Columba palumbus*). Only significant results ($p<0.05$) are presented.

Variable	System		Sex		Interaction		Comparison
	Pseudo-F	p	Pseudo-F	p	Pseudo-F	p	
BodySizePC1			30.17	0.0001			M>F
BodySizePC2	6.80	0.0056					C>A
HeadPC1							
HeadPC2	3.58	0.0438	4.57	0.0245			M>F; C>A
WingbonePC1	6.47	0.0095	25.28	0.0001	12.38	0.0002	
WingbonePC2							
WingexternalPC1	4.27	0.0324	17.76	0.0001			M>F; C>A
WingexternalPC2			4.20	0.033			F>M
PectoralPC1	50.47	0.0001			-1.54	0.0228	
PectoralPC2							
LegPC1	24.46	0.0001	19.57	0.0001			M>F; A>C
LegPC2							

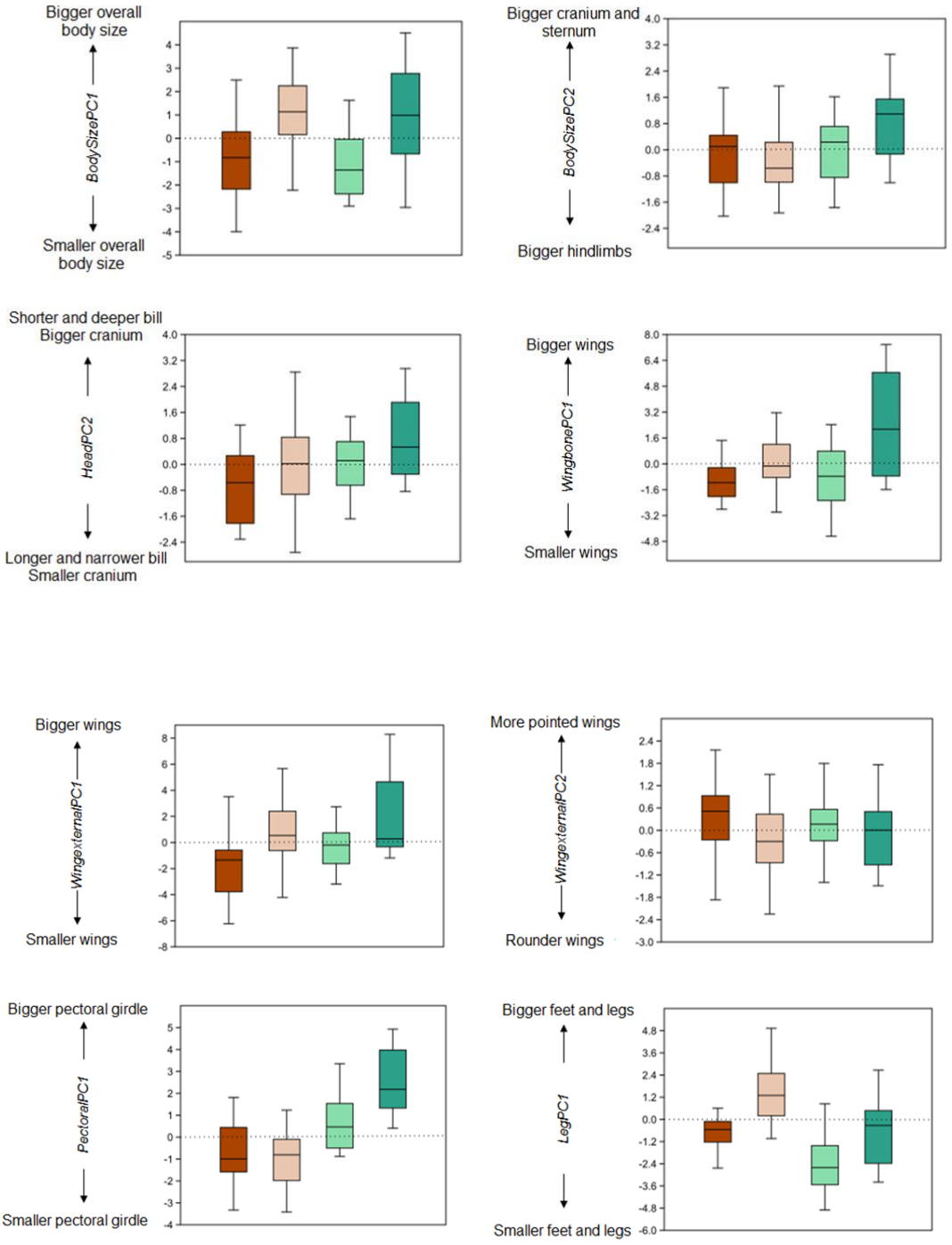

Figure 8- Differences between female and male insular birds and female and male continental birds regarding *BodysizePC1*, *BodysizePC2*, *HeadPC2, WingbonePC1, WingexternalPC2, PectoralPC1* and *LegPC1* values.

4- Discussion

4.1- Evolution of colouration in the Azorean woodpigeon

While comparing both populations and sexes for multivariate overall brightness, our results confirm that the insular *C. p. azorica* is less bright than the continental European *C. p. palumbus* in most regions of the body analysed. This is in accordance with what Hartert and Ogilvie-Grant (1905) found and with other studies that showed insular birds to be less bright and darker than the continental counterparts (Grant, 1965; Fitzpatrick, 1998; Figuerola and Green, 2000; Rising *et al.*, 2009; Roulin and Salamin, 2010; Fabre *et al.*, 2012; Doutrelant *et al.*, 2016). This decrease in brightness on islands is expected due to the poorer indirect fitness profits of mate choice (Petrie *et al*., 1998), which may be caused by reduced genetic diversity (Frankham, 1997; Griffith, 2000; Badyaev and Hill, 2003) and long term pair bonds, with increased parental care and longevity which leads to reduced investment in costly signals (Figuerola and Green, 2000; Botero and Rubenstein, 2012; Covas, 2012*).* Even though no work showing a clear correlation between Gloger's rule and colouration on islands was found, Gloger's rule may also have something to do with these colour patterns, in this particular case, since it postulates that animals that inhabit humid climates tend to be darker than those from dry areas, perhaps as an adaptation to a different vegetation structure and habitat luminosity (Zink and Remsen, 1986; Proctor and Lynch, 1993; Burtt and Ichida, 2004; Cuthill, 2015; Roulin and Randin, 2015; Friedman and Remeš, 2017), as well as a result of the increased resistance to dark feathers to bacteria (Burtt and Ichida, 2004). Since a lot of Azorean woodpigeon populations reside in Laurel forest which is a type of humid subtropical forest present in Macaronesia, the effect of Gloger´s rule in the woodpigeon might be a possible fact to be added.

Regarding brightness, univariate analyses showed that lower chest was the only body part with differences between sexes, with females being brighter than males. Results of other studies, with other columbids, suggest the opposite (Mahler and Kempenaers, 2002; Valdez and Benitez-Vieyra, 2016), with females apparently showing a tendency to choose males with the brightest plumage (Hill, 1993; Siitari *et al.*, 2002; Jawor and Breitwisch, 2003). The lack of differences between female and male on brightness and intensity, in most of the body is indicative of reduced sexual selection on colouration.

Regarding colour, females display higher spectral saturation and red chroma values while males show higher UV chroma values. According to univariate analysis only the crown, upperback and chest show higher UV saturation (chroma) in males

than females, which indicate that this is more prevalent in body regions possibly involved in sexual selection in the woodpigeon (Gibbs *et al*., 2001). Previous studies also showed this pattern of male columbids displaying higher UV reflectance than females, especially in body regions linked to sexual courtship (Mahler and Kempenaers, 2002; Valdez and Benitez-Vieyra, 2016). The explanation for the more saturated colour in females may be the same to the previously mentioned brightest plumage in females (low overall sexual selection in colouration). The fact that these differences between sexes are more pronounced in the continent is in accordance with studies that have demonstrated that there is less sexual dimorphism on islands, with bird species tending to develop monomorphic plumage across the sexes due to monogamy, increased population densities and biparental care (Badyaev and Hill, 2003; Roulin and Salamin, 2010; Doutrelant *et al.*, 2016).

The intense blueness in continental birds and less blue saturation (chroma) in the Azorean subspecies may explain the more vinous and thus less blue tone in the Azorean woodpigeon referred by Hartert and Ogilvie-Grant (1905). The absence of differences between sex and subspecies in the undertail coverts with regard to the univariate analysis indicates that it may be an area with less importance in inter and intraspecific communication.

4.2- Morphological evolution of the Azorean woodpigeon

According to the island rule, for small-sized colonizing birds there is an evolutionary trend towards larger body sizes in island populations and the opposite for colonizing birds of larger size (Clegg and Owens, 2002; Lomolino, 2005; Clegg *et al.*, 2008; Mathys and Lockwood, 2009; Roulin and Salamin, 2010; Boyer and Jetz, 2010; Melo *et al.*, 2017). Insular columbids tend to be bigger than the mainland counterparts (Millener and Powlesland, 2001; Worthy and Wragg, 2008; Monceau *et al.*, 2013). However, in the present study no differences between insular and continental populations were discernible on overall body size. One possible justification is that there are no selective pressures that lead to changes in body size in this particular case. An alternative hypothesis is that there was not enough time for any differences in overall body size to occur, but unless colonization was very recent this is probably not likely, as studies show that phenotypic change of this type can be very fast (Grant and Grant, 2002; Mathys and Lockwood, 2009; de Amorim *et al.,* 2017).

According to the present study's results, the woodpigeon presents sexual dimorphism in body size, with males being bigger than females, as previously reported by Huallacháin and Dunne (2010). This pattern may be caused as a result of sexual

selection associated with male to male competition for females and bigger size in males may be an indication of male quality, as this has been shown previously for other species of birds (Price, 1984).

Regarding the comparison of the head and bill size, no significant differences between subspecies or sexes were observed. The differences observed in head and bill shape suggest that males have deeper but shorter bills as well as bigger craniums than females. These results are congruent with the univariate analyses that showed males to have longer mandibles and higher craniums. It seems that there is notorious sexual dimorphism in the bill that may be caused by different feeding behaviours (Selander, 1966; Radford and Du Plessis, 2003; Temeles *et al.,* 2009), protection of the territory (Mínguez *et al.*, 2001) or mating (Coulter, 1986).

Differences between subspecies were found in the multivariate analyses of the head and bill as well as in the univariate comparison indicating differences in the head between insular and continental subspecies with continental birds displaying wider craniums and insular populations longer bills, something described in other bird studies comparing continental and insular populations (Carrascal *et al.*, 1994 Millener and Powlesland, 2001; Clegg and Owens, 2002; Mathys and Lockwood, 2009; Wright and Steadman, 2012). This change in bill shape can have several explanations such as different diets (Millener and Powlesland 2001), different foraging techniques needed to obtain food in the island (Wright and Steadman 2012), the reduced interspecific competition driving the evolution towards a generalist niche and diet (Clegg and Owens 2002; Mathys and Lockwood, 2009; Wright and Steadman 2012) or even due to increased intraspecific competition (Luther and Greenberg, 2011).

Univariate and multivariate analyses showed that males present bigger wings than females and continental birds presented larger wings and pectoral girdle than the insular subspecies. Again, this confirms the pattern described by Hartert and Ogilvie-Grant (1905), who claimed that the Azorean woodpigeon featured an apparent smaller wing size than the continental population. Shorter wings in islands birds are indeed expected since that, in islands, populations tend to become sedentary (Grant, 1965; Winkler and Leisler, 1992; Senar *et al.*, 1994; Lockwood *et al.*, 1998; Berthold, 1999; Copete *et al.*, 1999; Roulin and Salamin, 2010). However, no difference in wing shape between subspecies was found in this study. This absence of differentiation in the flight apparatus of birds between sedentary insular populations and migratory continental ones has been referred before by Komdeur *et al*. (2004), and according to the authors the insular species (the Seychelles' warbler) still had the ability for long-term flight, but could possess a behavioural impediment to cross big water masses. Another possible explanation could lie in our sampling: our continental sample is mainly composed by

Iberian and French individuals, whose populations are probably resident or partially migratory, what can explain this lack of differences. There were however differences between females and males with females displaying more pointed wings. One plausible explanation is that display flights executed by male woodpigeons (Cramp, 1958) require more manoeuvrability and consequent more rounded wings. Manoeuvrability might be also favoured in males for efficient territory maintenance (Vanhooydonck *et al.*, 2009).

In the particular case of the alula's length, there are bigger values in insular birds, what seems to agree with the results of other studies, that show an association between a smaller alula length and i) an increasing migratory behaviour (Fiedler, 2005), and ii) a higher aspect ratio of wings (Álvarez *et al*., 2001). A bigger alula seems to be more efficient in conditions when manoeuvrability is important (Álvarez *et al*., 2001), which is coincident with the Azorean woodpigeon's status as a sedentary bird. Regarding another trait associated with aerodynamic performance, tail length, no differences were observed between the two woodpigeon subspecies, with only males displaying bigger tails than females. However, this could either be associated with a function in sexual displays (Fitzpatrick, 1999), or just simply be a reflex of an overall bigger body size in the males of the species.

Mainland birds have relatively larger pectoral girdle bones (sternum, furcula and coracoid). This is expected given that these structures support the main flight muscles, the pectoral and the supracoracoideus (Calmaestra and Moreno, 2000; Tobalske and Biewener, 2008, Kaiser, 2010), thus augmenting considerably flight performances. This has been shown in previous studies comparing migratory and sedentary populations, including insular birds (Clegg and Owens, 2002; Egbert and Belthoff, 2003; Dietz et al., 2007; Wright and Steadman, 2012; Wright et al., 2016), while smaller pectoral muscle sizes in sedentary island populations may also be explained by resource limitation and subsequent decreased metabolic rates (Proctor and Lynch, 1993; Lomolino, 2005; Wright and Steadman, 2012). However, an interaction was observed (as well as in the wing bones) reinforcing the idea that differences between sexes were more pronounced in the continent than in the Azores. One possible explanation is that continental individuals, especially migratory ones, may display flight-related morphological differences between sexes linked to different migratory behaviour. However, if this was the only explanation we would notice a similar trend in wing shape (males would have both more developed flight-related bones and more pointed wings), but we actually see an opposite trend for wing shape (males have rounder wings, as previously discussed). Also, in species in which sexes show differential migration it's

the females that tend to migrate for longer distances (Catry et al. 2006). Possibly a more reasonable explanation implies a trade-off between aerodynamic performances for long-distance migration/dispersal versus exhibitions. In the continent males have rounder wings due to display flights, but still need to fly long distances (especially migratory populations), so compensate this with increased flight musculature (explaining the larger pectoral girdle bones). In the Azores, since there is no selection for long-distance flight performance, males do not need to enhance this musculature in comparison to females, and hence we still observe differences in wing shape but not in the skeleton.

Regarding the hind limbs, the Azorean woodpigeon has larger feet and legs. As a general pattern for birds, big legged species generally (but not always) spend more time on the ground or specialize in high speed terrestrial locomotion (Bennett, 1996; Zeffer *et al.,* 2003). This interpretation is similar to the one given by Millener and Powlesland, (2001), who linked bigger legs in the Chatham Islands pigeon with less volant, more terrestrial habits; conversely, the reduced size of the legs in continental individuals may be beneficial in reducing drag during flight (Pennycuick *et al.,* 1996). Our results also indicate that the ischium is deeper in Azorean birds. An enlarged ischium depth supports an increase in the size of leg muscles, a possible adaptation related to walking (Drovetski *et al.,* 2006) and thus, more cursorial habits.

5- Conclusions

Several studies have focused in how insularity shapes the phenotypic evolution of birds, in particular in morphology and colour. We hope with this study to both add to this general knowledge on insular biogeography, and shed light on the particular case of the Azorean woodpigeon, *C. p. azorica*, an endemic island taxa for which detailed studies are lacking. Our results are in accordance with several patterns described by previous work that compared insular and continental bird populations or species pairs, and show that Azorean birds are darker than the continental subspecies, which could be due to the decrease in sexual selection and environment conditions such as the luminosity of the habitat. Females and males showed no overall differences in brightness, but females showed higher spectral saturation, something that wasn´t expected and may be explained by reduced sexual selection on colouration in the woodpigeon. There is also a pattern of sexual dichromatism in the woodpigeon with

female birds displaying higher red chroma while males display higher UV chroma. These differences are bigger in the continent which may indicate that there is a tendency for monomorphism in the insular environment. Continental birds also appear to display higher blue chroma values than the Azorean woodpigeon.

Regarding morphology, male woodpigeons are bigger than females and exhibit bill shape differences to females. Several differences consistent with the adaptation to the insular environment were found, namely in the head with insular birds displaying longer bills (which could be linked to different diets and foraging techniques in the two environments) and smaller wings and pectoral girdle than the continental subspecies. In islands there is less predation and interspecific competition, which linked to the fact that a less developed flight apparatus is usually linked to the loss of migration may explain this pattern in the Azorean subspecies. Continental birds also show smaller legs, which is possible related to drag reduction for migration. Conversely, for the Azorean populations, bigger legs are also often related to more cursorial habits.

This work highlights the woodpigeon as a good model to study the evolution of birds in islands, allowing us to understand some adaptive changes induced by insularity, while also providing some updated information to be considered in future conservation planning. This work provides some evidence towards maintaining the endemic subspecies taxonomic status of the Azorean woodpigeon, with respective conservation and management implications.

In future work, a larger sample from each island and continental location should be analysed in order to perceive possible differences between islands and among different continental regions (for example, to analyse differences between migratory and sedentary continental specimens). The main difficulty in this work was to link the patterns observed with the specific behaviour and feeding of the Azorean woodpigeon since few studies have been conducted about this subject. During the dissection of the specimens, the gizzard and the crop were removed and stored in order to allow the analysis of diet, which together with the current knowledge will allow us to better link shifts in morphology with their proximate ecological causes.

6- References

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7- Appendix

Table A1- Specimens used in this study with sex, subspecies, sample sites and approximate coordinates.

Specimen	Sex	Subspecies	Sample site (country)	Sample site (region)	Approximate Coordinates
PAA040	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA041	M	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008016
PAA042	M	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA044	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA045	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA046	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA047	F	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA048	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA049	M	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA050	F	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA051	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA052	M	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA053	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA054	M	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA056	F	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA057	M	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA058	M	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA060	M	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA062	F	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA063	M	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA064	M	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA065	M	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA066	F	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA068	M	*C. p. azorica*	Portugal	Faial	38.592480, -28.734033
PAA069	F	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA072	M	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA073	M	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA074	M	*C. p. azorica*	Portugal	Pico	38.470055, -28.366117
PAA075	F	*C. p. azorica*	Portugal	Pico	38.470055, -28.366118
PAA076	F	*C. p. azorica*	Portugal	Pico	38.470055, -28.366119
PAA077	M	*C. p. azorica*	Portugal	Pico	38.470055, -28.366120
PAA078	M	*C. p. azorica*	Portugal	Pico	38.470055, -28.366121
PAA080	M	*C. p. azorica*	Portugal	Pico	38.470055, -28.366122
PAA083	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA084	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA086	F	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA087	M	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA088	F	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA089	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA090	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA091	F	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA092	M	*C. p. azorica*	Portugal	São Jorge	38.658865, -28.076329
PAA093	M	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA094	F	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA095	F	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA096	F	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA097	M	*C. p. azorica*	Portugal	Graciosa	39.048006, -28.008017
PAA098	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA099	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA100	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA101	F	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA103	F	*C. p. azorica*	Portugal	Pico	38.470055, -28.366117
PAA104	M	*C. p. azorica*	Portugal	Pico	38.470055, -28.366117
PAA105	F	*C. p. azorica*	Portugal	Pico	38.470055, -28.366117
PAA107	F	*C. p. azorica*	Portugal	Pico	38.470055, -28.366117
PAA108	M	*C. p. azorica*	Portugal	Pico	38.470055, -28.366117
PAA109	M	*C. p. azorica*	Portugal	Pico	38.470055, -28.366118
PAA110	F	*C. p. azorica*	Portugal	Santa Maria	36.972348, -25.117512
PAA111	F	*C. p. azorica*	Portugal	Santa Maria	36.972348, -25.117513

Specimen	Sex	Subspecies	Sample site (country)	Sample site (region)	Approximate Coordinates
PAA112	M	*C. p. azorica*	Portugal	Santa Maria	36.972348, -25.117514
PAA113	F	*C. p. azorica*	Portugal	Santa Maria	36.972348, -25.117515
PAA115	M	*C. p. azorica*	Portugal	Santa Maria	36.972348, -25.117515
PAA117	F	*C. p. azorica*	Portugal	Santa Maria	36.972348, -25.117516
PAA118	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA121	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA123	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA124	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA125	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA126	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA127	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA128	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA129	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA130	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227689
PAA131	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA132	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA134	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA135	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA136	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA137	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA138	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA139	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA142	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227689
PAA144	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA146	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA147	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227689
PAA148	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA149	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA150	F	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA151	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA152	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227689
PAA153	M	*C. p. azorica*	Portugal	Terceira	38.711887, -27.227688
PAA156	F	*C. p. palumbus*	Portugal	Vila Real	41.296417, -7.735004
PAA158	M	*C. p. palumbus*	Portugal	Vila Real	41.296417, -7.735005
PAA159	F	*C. p. palumbus*	Portugal	Vila Real	41.296417, -7.735004
PAA161	M	*C. p. palumbus*	Portugal	Vila Real	41.296417, -7.735005
PAA164	M	*C. p. palumbus*	France	Eure	49.150008, 1.055277
PAA168	M	*C. p. palumbus*	France	Charente-Maritime	45.778296, -0.811869
PAA169	F	*C. p. palumbus*	France	Charente-Maritime	45.778296, -0.811870
PAA170	F	*C. p. palumbus*	France	Charente-Maritime	45.778296, -0.811871
PAA171	F	*C. p. palumbus*	France	Charente-Maritime	45.778296, -0.811872
PAA177	F	*C. p. palumbus*	France	Ortaffa	42.588594, 2.913050
PAA179	M	*C. p. palumbus*	France	Ortaffa	42.588594, 2.913051
PAA180	F	*C. p. palumbus*	France	Ortaffa	42.588594, 2.913052
PAA181	M	*C. p. palumbus*	France	Ortaffa	42.588594, 2.913053
PAA185	F	*C. p. palumbus*	Spain	Seville	37.386263, -5.982183
PAA186	F	*C. p. palumbus*	Spain	Seville	37.386263, -5.982184
PAA188	F	*C. p. palumbus*	Spain	Seville	37.386263, -5.982185
PAA191	M	*C. p. palumbus*	Spain	Seville	37.386263, -5.982186
PAA192	M	*C. p. palumbus*	Spain	Seville	37.386263, -5.982187
PAA195	F	*C. p. palumbus*	Spain	Seville	37.386263, -5.982188
PAA198	F	*C. p. palumbus*	Spain	Seville	37.386263, -5.982189
PAA199	F	*C. p. palumbus*	Spain	Seville	37.386263, -5.982190
PAA200	F	*C. p. palumbus*	Spain	Seville	37.386263, -5.982191
PAA202	M	*C. p. palumbus*	Spain	Seville	37.386263, -5.982192
PAA203	M	*C. p. palumbus*	Spain	Seville	37.386263, -5.982193
PAA204	M	*C. p. palumbus*	Spain	Seville	37.386263, -5.982194
PAA205	M	*C. p. palumbus*	Spain	Seville	37.386263, -5.982195
PAA207	M	*C. p. azorica*	Portugal	São Miguel	37.780708, -25.493643
PAA209	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140768
PAA210	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140769
PAA211	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140770
PAA212	F	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140771
PAA213	F	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140772
PAA214	F	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140773

Specimen	Sex	Subspecies	Sample site (country)	Sample site (region)	Approximate Coordinates
PAA215	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140774
PAA216	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140775
PAA217	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140776
PAA218	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140777
PAA219	M	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140777
PAA220	F	*C. p. palumbus*	Denmark	Aarhus	56.192545, 10.140778
PAA221	M	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA222	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636375
PAA224	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636376
PAA226	M	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636377
PAA227	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA229	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636375
PAA236	M	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA257	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA259	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA260	F	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374
PAA261	M	*C. p. palumbus*	Portugal	Porto	41.161750, -8.636374

Table A2- Formulas used to calculate total brightness; intensity; red, blue and UV chromas and spectral saturation (from Hill and McGraw (2006)). *Rmax; Rmin*- maximum and minimum reflectance, respectively; *Ri*- reflectance at the *i*th wavelength (***λ***).

Variable	Formula
Total brightness	$\sum_{\lambda 300}^{\lambda 700} Ri$
Intensity	$Rmax$
UV Chroma	$\sum_{\lambda 300}^{\lambda 400} Ri \Big/ \sum_{\lambda 300}^{\lambda 700} Ri$
Blue chroma	$\sum_{\lambda 400}^{\lambda 500} Ri \Big/ \sum_{\lambda 300}^{\lambda 700} Ri$
Red chroma	$\sum_{\lambda 600}^{\lambda 700} Ri \Big/ \sum_{\lambda 300}^{\lambda 700} Ri$
Spectral Saturation	$Rmax / Rmin$

Table A3- Descriptive statistics of external and skeletal measurements of the woodpigeon (*Columba palumbus*). Values correspond to: mean ± standard deviation (n), amplitude (minimum - maximum). Every measurement is in mm. S1 - first secondary (the outermost); P1 to P10 - Primaries, numbered from body toward the wing tip.

	Azores		**Europe**	
	Males	**Females**	**Males**	**Females**
Wing	250,69 ± 5,82 (29) 240-262	245,62 ± 6,30 (26) 229,5-256	254,22 ± 9,33 (9) 240-270	249,63 ± 6,11 (20) 236-261
Alula length	69,74 ± 2,47 (33) 65-75	68,07 ± 3,46 (34) 58-74,5	66,42 ± 6,86 (12) 48,5-74,5	65,09 ± 2,57 (21) 60-71
Tail	166,10 ± 6,85 (36) 149,5-185,00	158,83 ± 4,70 (29) 146,00-166,00	163,35 ± 7,99 (13) 144,00-175,00	159,25 ± 5,58 (22) 149,00-171,00
Head	59,75 ± 1,65 (38) 56,66-62,35	58,95 ± 1,70 (34) 55,49-61,61	59,23 ± 1,40 (11) 57,29-61,5	58,59 ± 1,57 (17) 55,25-61,5
Bill-skull	30,15 ± 1,33 (37) 27,12-32,64	29,46 ± 1,26 (34) 26,06-31,70	30,03 ± 1,06 (12) 28,08-32,24	30,10 ± 1,31 (21) 28,05-32,54
Bill-cere	13,69 ± 0,75 (38) 11,97-15,21	13,74 ± 1,03 (35) 11,74-16,10	13,82 ± 1,01 (12) 12,39-15,78	13,73 ± 0,61 (19) 12,76-15,39
Bill depth	6,82 ± 0,42 (39) 5,94-7,78	6,70 ± 0,39 (35) 5,85-7,39	6,63 ± 0,45 (12) 5,82-7,20	6,37 ± 0,45 (21) 5,07-7,20
Bill width	5,56 ± 0,34 (38) 4,75-6,50	5,57 ± 0,38 (33) 4,75-6,50	5,44 ± 0,48 (12) 4,70-5,96	5,16 ± 0,43 (21) 4,52-5,96
Tar length	34,19 ± 1,10 (38) 31,53-36,37	33,24 ± 0,74 (35) 31,92-34,96	33,39 ± 1,00 (12) 31,47-35,13	32,89 ± 0,63 (19) 31,75-34,02
Tar depth	5,79 ± 0,54 (38) 4,92-6,82	5,54 ± 0,49 (36) 4,77-6,73	5,60 ± 0,36 (12) 4,92-6,10	5,42 ± 0,38 (21) 4,90-6,44
Tar height	6,27 ± 0,52 (38) 5,08-7,59	6,29 ± 0,32 (31) 5,62-7,04	6,18 ± 0,45 (12) 5,67-7,26	6,10 ± 0,19 (19) 5,69-6,42
Foot span	73,85 ± 2,89 (39) 67,00-80,00	71,56 ± 2,11 (35) 68,00-76,00	71,35 ± 1,99 (13) 68,00-74,50	70,58 ± 2,83 (20) 65,00-75,00
Hind toe	18,28 ± 1,04 (40) 15,98-20,37	17,70 ± 0,92 (36) 15,39-19,35	18,54 ± 0,82 (12) 16,91-19,78	18,00 ± 1,12 (21) 15,50-19,74
Inner toe	22,28 ± 1,17 (40) 20,09-25,10	21,71 ± 1,24 (36) 18,54-24,14	20,97 ± 1,19 (12) 19,33-23,49	20,90 ± 1,65 (21) 16,57-23,49
Central toe	32,26 ± 1,70 (39) 28,24-36,60	31,43 ± 1,57 (36) 27,81-33,97	30,26 ± 1,72 (13) 27,96-33,47	30,52 ± 1,57 (21) 28,19-34,36
Outer toe	23,45 ± 1,49 (39) 20,96-27,43	22,99 ± 1,50 (36) 19,08-26,07	22,25 ± 0,69 (10) 20,49-23,11	22,51 ± 1,58 (21) 19,43-25,00
Cranium GL	58,02 ± 1,62 (38) 54,94-60,93	57,05 ± 1,75 (28) 53,76-59,65	58,23 ± 2,17 (15) 54,43-62,78	56,16 ± 1,46 (19) 53,67-59,52
Bill length	26,75 ± 1,07 (37) 23,11-28,58	26,47 ± 0,87 (31) 24,68-28,12	26,23 ± 1,03 (17) 24,31-28,61	25,43 ± 1,15 (22) 23,29-27,23
Cranium height	20,21 ± 0,62 (38) 19,00-21,75	19,99 ± 0,53 (27) 19,18-21,35	20,56 ± 0,49 (16) 19,50-21,58	23,45 ± 1,49 (21) 18,84-20,71
Cranium width	20,38 ± 0,72 (39) 19,00-22,00	20,04 ± 0,81 (30) 18,67-21,90	20,97 ± 0,71 (15) 19,76-22,37	20,57 ± 0,79 (19) 18,86-21,69
Mandible length	22,65 ± 0,99 (37) 20,17-24,97	22,20 ± 0,98 (28) 20,19-24,41	22,67 ± 0,95 (16) 20,68-24,17	21,77 ± 0,88 (20) 20,12-23,29
Sternum length	71,15 ± 1,96 (39) 67,59-74,53	70,59 ± 1,89 (34) 67,03-73,80	73,96 ± 2,23 (18) 70,54-77,96	71,80 ± 1,76 (19) 69,56-75,61
Keel depth	32,67 ± 1,40 (38) 27,75-35,05	32,50 ± 1,09 (35) 29,62-34,01	34,88 ± 0,78 (18) 33,70-36,36	33,82 ± 1,00 (21) 31,60-35,20
Keel crista	75,57 ± 1,99 (39) 71,46-80,00	75,34 ± 2,15 (35) 70,78-79,39	78,42 ± 2,69 (18) 74,00-82,00	76,49 ± 2,39 (20) 72,07-80,14
Furcula length	37,21 ± 1,50 (33) 33,96-40,25	36,49 ± 1,00 (23) 34,21-38,42	39,49 ± 1,17 (16) 37,17-41,98	38,23 ± 1,32 (23) 36,02-40,81
Coracoid GL	40,92 ± 0,92 (37) 39,11-43,30	40,48 ± 1,16 (36) 37,80-42,51	42,00 ± 1,56 (16) 39,99-44,88	40,74 ± 1,09 (23) 38,91-42,90
Coracoid Bb	16,33 ± 0,48 (37) 15,40-17,42	16,04 ± 0,56 (35) 14,86-17,26	17,01 ± 0,72 (16) 15,81-18,34	16,52 ± 0,62 (22) 15,07-18,17
Coracoid Db	9,31 ± 0,48 (37) 8,43-10,33	9,07 ± 0,42 (35) 8,08-10,11	9,68 ± 0,41 (17) 8,90-10,34	9,24 ± 0,57 (23) 8,51-10,38
Humerus GL	53,55 ± 1,02 (34)	52,20 ± 1,39 (33)	54,53 ± 1,31 (16)	52,51 ± 1,41 (21)

	Azores		Europe	
	Males	**Females**	**Males**	**Females**
	51,21-55,64	49,28-55,26	52,14-56,57	49,14-55,51
Humerus Bp	20,85 ± 0,57 (40) 19,40-21,76	20,38 ± 0,50 (32) 18,95-21,21	21,40 ± 1,26 (17) 18,58-23,23	20,57 ± 0,74 (23) 19,29-22,02
Humerus Bd	12,93 ± 0,31 (37) 11,93-13,44	12,72 ± 0,30 (26) 12,16-13,20	13,18 ± 0,56 (16) 12,17-14,18	12,68 ± 0,43 (24) 11,70-13,30
Humerus SC	6,32 ± 0,30 (39) 5,91-7,51	6,18 ± 0,26 (34) 5,63-6,81	6,46 ± 0,27 (18) 5,94-7,01	6,24 ± 0,31 (25) 5,77-6,97
Radius GL	55,20 ± 1,30 (38) 52,48-57,93	54,03 ± 1,21 (34) 52,26-56,75	55,24 ± 1,47 (18) 52,57-57,28	54,17 ± 1,31 (22) 52,28-56,65
Radius SC	2,65 ± 0,14 (38) 2,42-3,01	2,58 ± 0,11 (33) 2,35-2,80	2,66 ± 0,17 (18) 2,44-3,05	2,56 ± 0,12 (22) 2,37-2,82
Radius Bp	5,69 ± 0,23 (40) 5,20-6,15	5,60 ± 0,22 (36) 5,09-5,91	5,55 ± 0,27 (18) 5,14-6,02	5,38 ± 0,34 (25) 4,62-6,35
Radius Bd	5,47 ± 0,24 (39) 4,95-6,06	5,36 ± 0,23 (36) 4,86-5,86	5,62 ± 0,29 (17) 5,22-6,31	5,27 ± 0,31 (25) 4,68-6,05
Ulna Did	8,08 ± 0,25 (40) 7,46-8,49	7,89 ± 0,29 (36) 7,21-8,37	8,19 ± 0,33 (17) 7,56-8,67	7,99 ± 0,27 (25) 7,47-8,53
Ulna SC	4,20 ± 0,21 (37) 3,84-4,68	4,10 ± 0,16 (35) 3,72-4,42	4,18 ± 0,20 (17) 3,81-4,44	4,02 ± 0,23 (23) 3,59-4,60
Ulna Bp	9,39 ± 0,26 (38) 8,92-9,92	9,18 ± 0,23 (35) 8,80-9,66	9,65 ± 0,36 (17) 9,16-10,22	9,18 ± 0,31 (22) 8,45-9,95
Ulna GL	60,78 ± 1,46 (35) 57,57-63,77	59,40 ± 1,70 (34) 53,78-62,94	61,15 ± 1,60 (17) 57,83-64,58	59,88 ± 1,44 (20) 57,84-62,54
Carpometacarpus Did	9,04 ± 0,29 (37) 8,43-9,67	8,89 ± 0,20 (31) 8,58-9,26	9,12 ± 0,37 (15) 8,50-9,81	8,94 ± 0,37 (23) 8,14-9,56
Carpometacarpus Bp	10,94 ± 0,26 (29) 10,13-11,55	10,83 ± 0,44 (31) 9,91-11,75	11,15 ± 0,61 (17) 9,55-11,91	10,82 ± 0,29 (22) 10,15-11,34
Carpometacarpus GL	37,85 ± 1,05 (39) 35,38-39,89	37,29 ± 0,82 (35) 35,99-38,90	38,26 ± 1,05 (17) 36,20-40,01	37,36 ± 0,78 (21) 36,05-38,98
Pelvis length	47,02 ± 2,73 (39) 41,75-52,71	46,38 ± 2,02 (31) 40,63-49,56	46,29 ± 2,08 (17) 43,08-49,58	45,40 ± 2,52 (21) 39,49-48,54
Ischium depth	13,59 ± 0,62 (39) 12,35-15,10	13,32 ± 0,70 (35) 12,06-14,71	12,86 ± 0,68 (18) 11,28-13,88	12,45 ± 0,56 (23) 11,50-13,84
Tibiotarsus Bd	7,61 ± 0,26 (38) 7,02-8,04	7,39 ± 0,30 (36) 6,63-7,89	7,43 ± 0,27 (18) 7,02-7,99	7,17 ± 0,33 (24) 6,62-7,95
Tibiotarsus Dip	10,11 ± 0,31 (39) 9,37-11,10	9,89 ± 0,33 (35) 9,20-10,56	10,18 ± 0,40 (18) 9,74-11,11	9,54 ± 0,43 (25) 8,50-10,25
Tibiotarsus SC	3,81 ± 0,17 (39) 3,51-4,19	3,71 ± 0,16 (34) 3,40-3,99	3,83 ± 0,16 (18) 3,54-4,13	3,57 ± 0,19 (25) 3,18-3,85
Tibiotarsus GL	61,64 ± 1,68 (35) 58,27-65,22	60,09 ± 2,02 (32) 55,64-63,48	60,17 ± 1,58 (13) 57,70-62,14	59,70 ± 1,18 (20) 57,39-62,05
Femur Bd	8,85 ± 0,30 (39) 8,27-9,53	8,72 ± 0,29 (35) 8,30-9,39	8,69 ± 0,39 (18) 8,10-9,69	8,44 ± 0,29 (25) 7,97-9,06
Femur SC	4,06 ± 0,20 (37) 3,69-4,54	3,93 ± 0,19 (34) 3,61-4,52	4,00 ± 0,19 (18) 3,68-4,33	3,77 ± 0,18 (24) 3,39-4,10
Femur GL	46,05 ± 1,22 (37) 42,49-47,93	44,55 ± 1,19 (34) 42,32-47,21	45,53 ± 1,34 (17) 43,85-48,33	44,24 ± 0,92 (23) 42,19-45,85
Femur Bp	9,53 ± 0,31 (38) 8,76-9,99	9,28 ± 0,24 (35) 8,65-9,95	9,39 ± 0,26 (16) 8,93-9,92	8,97 ± 0,32 (25) 8,28-9,54
Tarsometatarsus Bd	8,71 ± 0,33 (39) 8,08-9,38	8,53 ± 0,23 (34) 8,13-8,89	8,63 ± 0,31 (17) 7,95-9,03	8,32 ± 0,32 (23) 7,76-9,02
Tarsometatarsus Bp	8,57 ± 0,35 (39) 7,81-9,51	8,32 ± 0,29 (36) 7,70-8,79	8,10 ± 0,32 (17) 7,52-8,68	8,10 ± 0,18 (20) 7,67-8,44
Tarsometatarsus SC	3,82 ± 0,24 (38) 3,30-4,26	3,76 ± 0,25 (36) 3,24-4,30	3,81 ± 0,24 (17) 3,36-4,21	3,66 ± 0,23 (24) 3,15-4,06
Tarsometatarsus GL	32,65 ± 0,95 (36) 30,82-34,00	31,77 ± 0,80 (30) 30,52-33,55	32,02 ± 1,12 (15) 29,38-33,70	31,42 ± 0,61 (18) 29,73-32,30
S1	124,59 ± 3,73 (37) 117,00-132,00	119,77 ± 4,96 (35) 110,00-130,00	123,42 ± 4,76 (13) 114,00-130,00	120,00 ± 2,54 (20) 115,00-123,50
P1	124,65 ± 3,40 (39) 116,00-131,00	120,64 ± 3,86 (35) 115,00-130,50	125,15 ± 3,74 (13) 119,00-133,00	121,95 ± 2,90 (20) 115,00-127,00

	Azores		Europe	
	Males	**Females**	**Males**	**Females**
P2	128,76 ± 3,21 (39) 121,00-136,00	123,50 ± 3,94 (36) 117,50-133,50	128,46 ± 3,69 (13) 124,00-137,00	126,16 ± 3,71 (22) 118,00-133,00
P3	132,63 ± 3,18 (38) 126,00-141,00	127,27 ± 4,02 (35) 121,00-135,00	133,96 ± 4,25 (13) 129,00-143,00	131,20 ± 2,72 (20) 126,50-136,00
P4	137,77 ± 3,66 (37) 130,00-150,00	132,80 ± 3,99 (35) 125,00-140,50	141,31 ± 3,41 (13) 137,00-149,00	137,53 ± 3,80 (20) 127,00-144,00
P5	147,01 ± 4,12 (35) 137,00-160,00	142,53 ± 4,02 (31) 134,00-151,00	150,21 ± 3,30 (12) 145,00-157,00	146,47 ± 3,70 (17) 138,00-152,00
P6	159,28 ± 3,75 (37) 151,00-169,00	156,44 ± 4,68 (34) 148,00-166,00	161,33 ± 5,69 (12) 148,00-171,00	157,59 ± 4,12 (17) 149,00-163,00
P7	173,01 ± 5,30 (39) 161,00-187,00	169,95 ± 4,41 (33) 162,00-179,50	176,54 ± 5,79 (12) 167,00-185,00	172, 47 ± 5,68 (19) 164,00-184,00
P8	183,28 ± 4,81 (38) 171,50-195,50	178,68 ± 4,41 (33) 169,00-187,00	184,58 ± 6,53 (13) 176,00-198,00	182,50 ± 5,81 (18) 174,00-200,00
P9	178,89 ± 4,56 (31) 171,00-189,00	177,46 ± 4,36 (27) 168,50-187,00	181,05 ± 6,65 (11) 171,50-191,50	178,87 ± 4,16 (19) 172,50-186,00
P10	167,05 ± 5,56 (28) 153,00-176,00	163,64 ± 3,79 (29) 157,00-171,00	168,75 ± 6,09 (12) 158,50-175,00	166,16 ± 2,56 (16) 161,50-171,00